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and observational analysis of
conflict in humans and animals**

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EDITORIAL

The council of the International Society for Research on Aggression asked me to take over the task of Editor-in-Chief of Aggressive Behavior at the Biennial ISRA Meeting in October 1978. I am happy to do so. The task is made easier by the work of my predecessor, Kenneth Moyer, who very ably led the journal from the idea stage to its present position as a forum for the best work of scientists in a variety of fields. A new multidisciplinary journal has an unusual problem since it must become visible to investigators and readers in several fields, each of which has its own journals whose standards are known. I believe that Aggressive Behavior has now become established as a respected journal for a variety of researchers.

Inevitably, each editor of a journal helps to characterize it. My aim is to foster mutual interest and even a rapprochement among those who study aggressive behavior from social and biological perspectives. To this end, Stuart Tavol and Suzanne Steinmetz have agreed to become Associate Editors, joining Paul Brain and Alan Lehnert whose research has been mainly on the biological bases of aggression. Aggressive Behavior will continue to be a journal with a broad perspective, and I want to make sure that all researchers in aggression consider us as a real option when they want to publish something good. By having associate editors and an editorial board who represent many fields, I hope that even the most reluctant potential author can be persuaded thereby to entrust us with his or her opus magnum, confident that it will be reviewed by appropriate experts who are compassionate, tough-minded, yet fair. Having promised all that, we must now deliver in order for us to do so, we must receive manuscripts, especially from those areas which have been under-represented in the first four volumes of Aggressive Behavior.

I look forward to continued success of the Journal so capably published by Alan Liss and his staff. Remember that membership in ISRA decreases the cost of your subscription substantially.

Ronald Baerninger
Editor-in-Chief

Aggressive Behavior of Pigeons Suppression by Archistriatal Lesions

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The agonistic responses of pigeons to the introduction of a stick and the experimenter's hand into their home cages is described. The effects of lesions of the archistriatum, a presumed homologue of the mammalian amygdala, of lesions of the overlying neostriatum and of control sham operations on this behavior in selected aggressive pigeons are reported. Only archistriatal lesions lead to a persistent depression of the aggressive and a converse increment of the avoidance components of the pigeon's response to both test stimuli. The results are discussed in relation to other evidence on the role of the avian archistriatum and this structure's correspondence with the amygdala.

Key words: pigeon, archistriatum, intra/interspecific aggression

INTRODUCTION

Ethological studies show that the aggressive behavior of animals serves a variety of functions depending on the socio-ecological niche occupied by each species. Accordingly, it can be expected that the physiological mechanisms controlling aggression will differ from species to species. A common phyletic origin may conversely have caused the retention of similar patterns of control. It is obvious that comparative studies on the physiological basis of aggression are needed to assess the effect

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sequel is aggression. Freezing is a fear response that will often develop from the attentive response: the animal simply becoming immobile and remaining so for a period varying between several seconds and minutes before slowly beginning to make small amplitude movements or before suddenly exploding into extreme flight behavior. From attention or such unfreezing pigeons often progress to leaning away: that is bending the body and head away from the stimulus with a sideways orientation without shifting and while observing the stimulus intently. In this position it may hold out the wing closer to the stimulus: wing fending. This may lead to withdrawing: that is walking away mostly with a sideward attitude to the stimulus and attempting frantically to leave the cage: pushing against the wire netting. Attempts to fly away may then be observed: the birds extending and flapping the wings and pushing against the cage walls. This active flight behavior is sometimes, though not often preceded by alarm calls: harsh notes transcribable as *hinnh*. A variant style of avoidance and escape is crouching: when the pigeon presses the body against the floor: the wings drooping slightly and the neck retracted: and sneaking: where it crawls away maintaining this posture.

A distant stimulus often elicits bow-cooing: that is walking: tracing a series of reversing semicircles with the plumage fluffed: the tail spread and the throat swollen with interspersed brief bursts of speed and body and head bows while giving repeated calls: *cooo-cooo*. If the stimulus approaches the animal will usually revert to threat. The animal fluffs the plumage: sometimes also spreads the tail and swells the throat maintaining a sideways orientation to the stimulus. The wing opposite to the stimulus is raised above the back: that close to the stimulus is flicked or more rarely also raised. This may lead to attack where the animal approaches the stimulus: sometimes jumping forward and slapping with the wing close to the stimulus: exception with both wings raised: them and bringing them down sharply on it. It will also peck: most short of target but sometimes gripping the stimulus vigorously: shake it or twisting it with the eyes closed. A deep throated aggressive vocalization may accompany this behavior.

For the final routine: scoring the response of a pigeon to a stick or hand test was classed as either attack: threat: retreat or flying away depending on the response predominantly shown by the subject. In the great majority of the tests there was no difficulty in deciding between the categories. The interobserver agreement was of the order of 95%. Additionally we also noted which of the behavior elements described above were shown during each test component. Later in the text we will also often refer to aggressive and avoidance behavior: these categories simpler for to attack and threat: and retreat and flying away respectively taken together.

We compared the efficacy with which the two stimuli used: stick and hand: elicited aggressive responses from the initial 75 animals not yet selected for predominant aggressive responding. The stick elicited more aggressive responses than the hand in only 5% of the pigeons while the hand did so more than the stick in 64% of the subjects: the remainder of the subjects reacting similarly to both.

stimuli. Figure 1 shows that the tests with two stimuli elicited different response profiles. The hand released relatively more attack, retreat and flying away scores than the stick which yielded predominantly threat while relatively few tests yielded no agonistic responses at all.

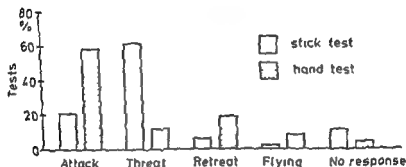


Fig. 1. Agonistic behavior shown by pigeons ($N = 75$) in response to a stick and a hand introduced into their home cages.

Lesions

The examination of the histological sections revealed differences in the location and extent of the lesions in the 12 experimental animals. This made it necessary to class them into three groups: three subjects had bilateral lesions in the archistriatum, three others had only unilateral lesions in the same structure (it is possible that very small contralateral lesions might have passed undetected), six subjects had bilateral lesions that largely spared the archistriatum and mainly affected the overlying neostriatum caudale (Fig. 2). Additionally, there were six subjects in the control group that had undergone a sham operation; their brains were histologically normal.

Comparing in each case the percentage response scores on both the stick and the hand tests four weeks preoperatively and five weeks postoperatively reveals that both the bilateral and the unilateral archistriatally damaged animals showed reasonably similar decrease in aggressive behavior and increase in avoidance behavior (Fig. 3). This warranted lumping them together into a single group of archistriatals. Due to chance several subjects with preoperatively less marked aggressive and more pronounced avoidance behavior were included in this group. Nevertheless, all the archistriatally lesioned pigeons showed a postoperative decrease in aggression and an increase in avoidance behavior. The animals with neostriatal lesions showed no

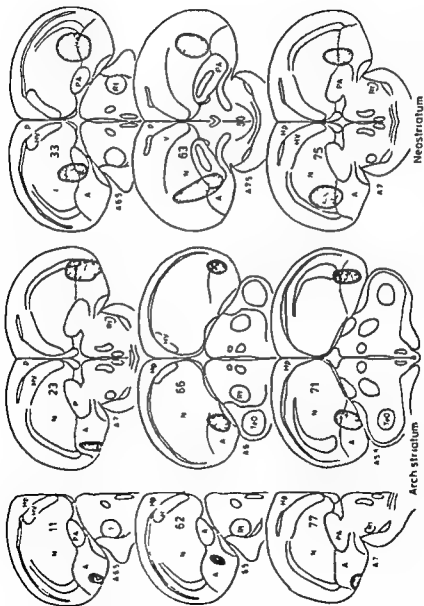


Fig. 1. Location of the archistriatal and neostriatal brain lesions. Only a sample of neostriatal lesions is shown in the three middle plates. Numbers identify the subjects.

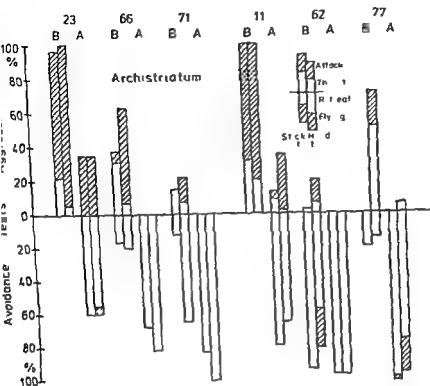


Fig 3 Agonistic behavior shown by pigeons during tests before (B) and after (A) lesions of archistriatum. Numbers identify individual subjects

change in behavior unless it was a slight average increase in aggression (Fig 4). The control subjects overall similarly did not show changes except that one animal (No 16) yielded an unexplained delayed and transitory postoperative decrease in aggression and increase in avoidance (Fig 5).

Figure 6 illustrates the mean results of all three groups. Comparison of the preoperative with the postoperative behavior separately for the stick and the hand tests reveals that only the archistriatally lesioned animals showed significant changes. The decrease in aggression in the hand test was significant at $P < 0.01$ ($t = 5.43$, $df = 5$). The increase in avoidance was significant for both the stick test ($t = 4.92$, $df = 5$) and the hand test ($t = 5.59$, $df = 5$) at $P < 0.01$.

The nature of the response changes in the archistriatally lesioned animals is shown in more detail in Figure 7. Excepting some of the more rarely occurring patterns for which the evidence is not clear, all other patterns showed changes compatible with the overall conclusion that the lesions produced a decrease in aggressive and an

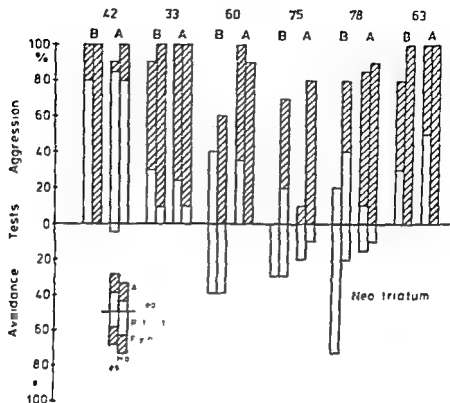


Fig. 4. Aggression behavior shown by pre- and post-operative tests before (B) and after (A) lesions of the neostriatum. Numbers given by individual subjects.

increase in avoidance behavior. In particular pecking and wing slapping decreased and leaning away and flinching increased as a consequence of partial ablations of the archistriatum. However the effects of the archistriatal lesions on the agonistic behavior may not be permanent. Figure 8 shows that by the sixth postoperative week the subjects' responses partially the aggressive components returned some way towards preoperative levels. We do not have sufficient data available to decide what the time until recovery is dependent on the size of the lesion but this seems possible. Since the histology showed that the lesions were filled with glial scar tissue capable of neural function, it must be concluded that other neural tissue must have been responsible for this recovery.

Regarding food consumption there was only a rather slight difference between archistrially lesioned and the controls (unlesioned and neostrially lesioned). Both groups showed a transitory about 10% decrease in food intake after the intervention. This decreased intake may have been more pronounced in the archistrially lesioned subjects (three weeks) than in the controls (two weeks). This difference did not show up in the body weights which increased equally in both groups by about 5% in the first two weeks after surgery.

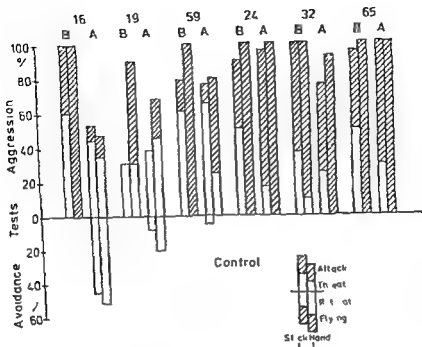


Fig 5 Agonistic behavior shown by pigeons during tests before (B) and after (A) control sham operations. Numbers identify individual subjects.

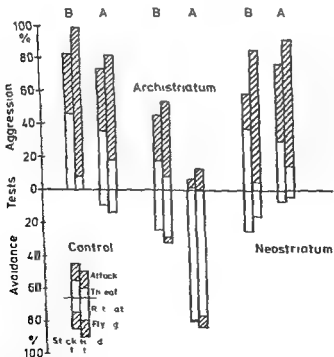


Fig 6 Mean agonistic behavior shown by pigeons (N = 6 in each group) during tests before (B) and after (A) archistriatal or neostriatal lesions and sham control operations.

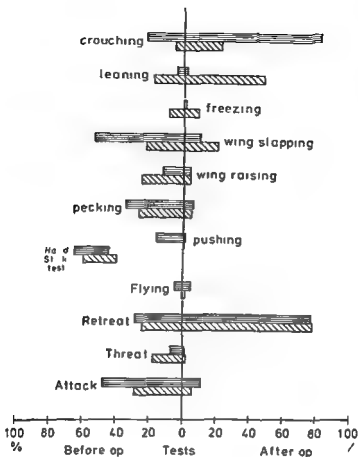


FIG. 7. Comparison of pre and postoperative agonistic behavior of archistriatales lesioned pigeons ($N = 6$).

DISCUSSION

Agonistic behavior is shown by animals in many different functional contexts. It may address members of other species as part of predatory behavior, as an anti-predator response, as a defense against parasites or as a reaction against ecological competitors. As a response to conspecifics it may function to secure or defend resources (including social partners) or to support or prevent intraspecific predation or even to reject diseased individuals. While the behaviors shown in these various situations by a given species may be qualitatively different, they often overlap. The functional context of the agonistic responses elicited by our testing procedures

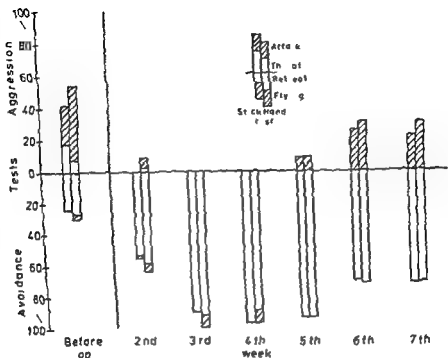


Fig. 8 Time course of agonistic behavior changes after archistriatal lesions in pigeons. Mean of six subjects

probably complex. On the one hand it may be understood as an interspecific anti predator behavior as indicated by the occurrence of freezing, crouching and sneaking responses shown in the wild toward predators but rarely against conspecifics [Delius unpublished observations]. On the other hand there are indications that this domestic species considers man to some extent as a conspecific much as imprinted geese do their caretaker. This is suggested by the occurrence of bow-cooing, a response that is not shown toward natural predators by pigeons but is very frequent in intraspecific social encounters both agonistic and sexual. Our tests may thus assay a functionally heterogeneous set of behaviors that conceivably could also involve different control substrates.

These considerations however will provisionally be subordinate in view of the simplicity and relative reliability of the tests. Their usefulness is justified by the results. Lesions located in the archistriatum markedly and significantly depress the aggressive responses in favor of a predominance of avoidance behavior as measured by the tests. Lesions in the neostriatum do not have this effect rather there may

be a slight though nonsignificant increase in aggressive behavior. Note that this group of animals provided a blind control group since only the histology revealed that the intended archistriatal lesion had been misplaced. Control sham operated animals did not show any significant change.

The reduction in aggression and increase in avoidance following archistriatal lesions contrasts somewhat with results obtained on birds by other authors. Phillips [1964] reported taming as the main consequence of ventromedial archistriatum and tractus occipito mesencephalicus lesions in mallards (*Anas platyrhynchos*), the tract being the main efferent pathway of the archistriatum. The descriptions seem to suggest that taming consisted principally of a reduction of fear responses elicited by man. He also obtained comparable results with similarly lesioned lovebirds (*Agapornis roseicollis*); fear inducing objects were less effective in suppressing feeding. However there was also reduction in mobbing behavior toward such objects, mobbing being perhaps a partially aggressive response [Phillips 1968]. Zeier [1968] refers to the taming effect of more lateral archistriatal lesions in pigeons (corresponding more closely to ours) but does not specify of what this taming consisted. Anterolateral lesions seemed to increase fearfulness, occasionally aggressiveness [Zeier 1971]. Maser et al. [1973] report that archistriatal lesions in chickens (*Gallus gallus*) facilitate the tonic immobility response that we think to be related to freezing behavior, an avoidance response. Dafters [1975, 1976] reports a learning deficit in archistriatally lesioned pigeons when an aversive reinforcer was used (compare also Cohen [1975]). Wright and Spencer [1976] found that ring doves (*Streptopelia risoria*) with tractus occipito mesencephalicus transections virtually ceased to show any kind of agonistic behavior to a predator model.

It does indeed not seem possible to ascribe consistently to the archistriatum an aggression facilitating/avoidance suppressive function. Several factors may be responsible for the apparent diversity in the results of these various studies: variations in lesion extent and location, species differences, and heterogeneous behavioral assessment. In our case we also wonder whether the selective use of aggressive animals might not have biased the results. Elsewhere one of us has argued that the same neural substrates might have different functions in the control of fear and aggression in individuals with either fearful or aggressive dispositions [Delius 1973]. Could it be that the same lesion might suppress aggression and facilitate avoidance in an aggressive subject but have the reverse effect in a fearful one?

Collation of information from electrical brain stimulation studies on various avian species suggests that indeed the bird's archistriatum, among other structures, is a control substrate for both aggression and avoidance responses [Akerman 1966, pigeons; Maley 1969; Phillips 1964; mallard; Putkonen 1966, 1967, 1973; Phillips and Youngren 1971; chicken; Vowles and Beazley 1974; ring doves]. Though not decisively, these heterogeneous data seems to indicate that the aggressive responses are obtained predominantly from the ventromedial part of the archistriatum, whereas avoidance responses are elicited from more dorsolateral parts of the structure.

Such a differentiation in function might relate to the regional connectivity differentiation that Zeier and Karten [1971] have established for subdivisions of the pigeon's archistriatum [see also Zeier and Karten 1973 Kondo 1933 chicken]. Our lesion data are insufficient to allow conclusions as to correlations between the intersubject behavior defect differences and the rather small variations in lesion placement. That is an issue that must be pursued in further work. The feasibility of such an analysis is suggested by the fact that small lesions only affecting reduced portions of the archistriatum yielded clearcut behavioral effects. A remarkable finding is that unilateral archistriatal lesions and small ones at that seem just as effective in reducing aggression as bilateral lesions. As a rule unilateral lesions lead to lesser and sometimes hardly detectable behavioral defects as compared with symmetric lesions. There are cases however in which the effect of such lesions is more marked than that of bilateral ablations. An example is unilateral hemispherectomy in the chaffinch (*Fringilla coelebs*) that leads to a predator mobbing response deficit to stimuli viewed with the contralateral eye. An equivalent deficit is not apparent with symmetric lesions [Strata 1964]. The phenomenon may apply to the archistriatum since Kalisher [1905] reports a contralateral visual agnosia following unilateral lesions of this structure in parrots (*Psittacidae* sp). However we did not notice such a lateralization effect. Aggressive responses to the test stimuli were reduced seemingly no matter with which eye the animal viewed them but admittedly no detailed attention was given to this point.

It remains to comment on the absence of marked alteration of the feeding behavior of the archistriatally lesioned animals as compared with their controls. Archistriatal lesions in pigeons have been reported to lead to temporary aphagia by Zeigler et al [1969]. This fits with the archistriatum anterior being a projection of the nucleus basalis, a structure that undoubtedly plays a role in controlling food uptake responses [Zeigler 1976]. Our lesions almost certainly spared the relevant portion of the archistriatum and this may explain the slightness of the feeding deficit we obtained. The homology of the avian archistriatum and the mammalian amygdala is supported in a general way by the results of lesions and stimulation experiments in birds. The behavioral syndromes obtained correspond to those often found in equivalent studies in mammals. Amygdala lesions have variously affected aggressive and avoidance behavior [eg Kaada 1972], food intake [eg Fonberg 1974 Box and Mogenson 1975] and predatory behavior [eg Zagrodzka and Fonberg 1977 Karli et al 1977]. Stimulation on the other hand has been shown to elicit or at least facilitate aggression avoidance [eg Fernandez de Molina and Hunsperger 1962 Delgado 1967] predatory aggression [eg Egger and Flynn 1963] and feeding [eg Fonberg and Delgado 1961 Lewinska 1968]. A recurring theme in these studies however is the functional differentiation of the amygdala in some cases coinciding with recognizable anatomical subdivisions. It is premature to relate this to the situation in birds. Zeier and Karten [1971 1973] have shown that the archistriatum is differentiated anatomically and actually they argue that the more lateral and anterior portions

may not be homologous to the mammalian amygdala at all. The lesion and stimulation work described above contains some indications of a corresponding functional differentiation but the information available does not yet fit into a coherent pattern.

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Rank and Reproduction Among Female Langur Monkeys: Aging and Improvement (They're Not Just Getting Older, They're Getting Better)

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An investigation of the social rank, reproduction, and ages of adult female Indian gray langur monkeys (*Presbytis entellus*) living in two colony social groups revealed that rank based on displacements is neither correlated with nor best predicted by female age or reproductive value. The hierarchy of female ranks is best conceptualized as a layered ranking system in which there are clusters of females of the same dominance rank forming layers within the structure. Statistical significance in frequencies of displacement differs between but not within these layered groups of females. Factors such as group composition, presence of uterine kin, reproductive state, and individual personality are hypothesized to predict changes in female rank far better than does reproductive value. Our data show that reproductive success increases with age. The infant survival record for the six oldest females in our colony was much better than for the five youngest adult females.

Key words: langur monkey, aggression, dominance, reproduction, selection, age

INTRODUCTION

For several decades the social behavior of Old World monkeys and apes has been scrutinized by investigators from several disciplines, many seeking models

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of human evolution and illustrations of natural selection including kin and sexual selection. It has been known for many years that rank among males is important for reproductive success and hence for evolution. Yet it has only been in the last few years that investigators have called attention to the possible importance of social rank for the reproductive success of females [Missakian 1972 Drickamer 1974 Blaffer Hrdy and Hrdy 1976 Blaffer Hrdy 1976 1977 Deag 1977]. Earlier stages of primate research on baboons and macaques and particularly on the conspicuous males of some species produced a premature and over simplified picture not only of female behavior [Beach 1976] but also of primate behavior in general [Bernstein 1970 1976]. Social structure was conceptualized as rather uniform and to a large extent dependent upon social hierarchies which in turn promote the fitness of only the highest ranking individuals [Rowell 1972]. The relationship between rank and reproduction even among males appears to be ambiguous and much more complex than anticipated by early researchers [Hausfader 1975].

The purpose of this paper is to explore the relationships between age reproductive value reproductive success and social rank among female Indian langur monkeys (*Presbytis entellus*). At the same time we propose to call attention to special characteristics of the subfamily to which langurs belong the Colobinae. The Colobines or the leaf-eating monkeys are indeed the other half of the Old World monkeys and the subfamily encompasses as many genera and species as the well known Cercopithecinae and of the two the Colobines may prove to be the most variable. Langur social organizations and structures are extremely flexible inasmuch as both multi male one male bisexual and unisexual groups may be found within a local population. Jay [1963] and Yoshida [1968] stress that langur society is quite sensitive to its immediate environmental conditions and Curtin [1977] discusses in what specific ways this sensitivity can be expressed. Our data suggest that among female langurs relationships between rank age and reproduction are neither simple nor readily apparent. Based upon data from a study of two well constituted captive groups it was found that ranking female langur monkeys in a linear manner as though they were on rungs of a ladder obscured very important information about the nature of langur social structure. For example younger females frequently become actively involved in displacement a behavior traditionally associated with dominance or high rank but they are not highly successful. In contrast the most dominant females acted least frequently in dominance displacements but almost always more successfully than their often younger associates. Furthermore while it can be said that younger females have potentially higher but not yet proven reproductive values due to their age in our study groups older females (multipara) produce almost twice the number of viable offspring as young primiparous females. Data from field studies of free ranging langur monkeys support these conclusions [Jay 1963 Curtin 1975 Boggess 1976]. It appears that the attainment and expression of an

individual's social rank is exceedingly complex—sometimes subtly and/or infrequently exhibited—and may change within (relatively) short periods of time. A female's social rank is sensitive to events in her reproductive cycle and to the processes of aging. There are many strands to a social rank—far more than are reflected by, for example, contests between animals stimulated or elicited by the human observer.¹ Among many *Cercopithecines* but less so for *Colobines*, the system of rank relations among group members is an obvious component of the group social structure and is furthermore vital to the life strategies of individual animals.

SUBJECTS, METHODS AND PROCEDURES

This study was undertaken at the University of California (Berkeley) Animal Behavior Station and is based upon 311 hours of observation of females living in stable social groups which include some but not all close relatives. Issues raised in field work by Jay [1963 and unpublished data], Blaffer Hrdy [1977], Curtin [1975], Bogness [1976], and a considerable amount of colony data (over 4,000 observation hours at Berkeley and 1,500 in San Diego by McKenna [1975]) prompt us to address the phenomenon of social rank among females. To this end a subset of detailed focal animal samples of eleven colony living females (six feral or Indian born, five captive-born) were examined. Data were collected over a continuous eight-month period using focal animal samples ten minutes in length. A standardized behavioral repertoire and recording technique were employed by trained observers whose inter-observer reliability was greater than 0.95. Each of the groups containing our subject females included an adult male and immature individuals of both sexes.

The purpose of this study was to examine the concept of social rank among female langurs and to investigate the relationship between social rank, age, and reproduction. Two rank orders were established for females in each group. One set of ranks was based upon the sum total of displacements and move aways, two dominance-related behaviors. In the data analysis these two behavior items are combined and called displacements. A female (animal X) was said to displace another (animal Y) if upon her approaching female Y and after establishing visual or tactile contact, female Y departs, giving up to female X her previously held physical space or some other identifiable resource such as a food item or grooming partner. On those occasions when it was difficult to make a judgment as to the animal's intent or motivation and hence the displacement was ambiguous, a behavior category called a move away was used. A female X was said to move away from female Y if upon some social stimulus such as the approach of Y, female X departs from Y but without Y's subsequent appropriation of X's space or resource. To determine whether our displacement-move away-based ranking system reflected actual rank relationships, nine aggressive behavior items—bite, chase, hand threat,

hand threat with contact face threat glare threat slap ground lunge threat and nonsexual harassment — were added to the sum totals of displacement and move aways received and initiated by each of the females of both groups. A second set of ranks which included these dominance related aggressive behaviors was thereby constructed and then compared with the ranks based only upon our nonobserver provoked displacements and move aways. There were no differences between the two sets of ranks. Hence for comparative purposes we chose to work only with our displacement based ranks. It should be noted that when individuals moved independently of particular social stimuli as for example when a female departed from a relaxed resting cluster other behavior units (horizontal departure or vertical departure) were used and were not included as measures of rank.

Over 1 800 ten minute focal samples were analyzed. These samples were key punched and analyzed by an ALGOL computer program specially designed to tabulate frequencies of occurrences actors receivers and participants in interactions. DGS ECLIPSE computer system using R D O S was employed. To determine possible statistically significant differences between assigned ranks T tests at the 0 001 confidence level were used as well as regression coefficients.

Since the age of female langurs is critical in testing hypotheses of female reproductive strategies involving fitness [Blaffer Hrdy 1976 1977] it is important whenever possible to present confirmed and reliable age data. A number of external and easily observed physical characteristics including depth and quality of facial creases extent of facial and skin wrinkling (particularly around the nose) teeth wear and nipple and lip form have been used to approximate the age of subjects [Blaffer Hrdy 1977 72–76]. While some of these criteria have been used by other investigators to assess general but not specific age [Jay 1963] tremendous inter individual variability in any one of these traits makes differentiating between for example old and middle aged [Blaffer Hrdy 1977] females living in the field a very subjective and inexact procedure. A captive setting provides both a controlled environment for quantification of behavior and an opportunity to obtain records important for testing possible relationships between age and other phenomena such as status and reproduction.

The exact age of five of our subject females is known from birth records and estimates were made on the remaining six feral born females. It is very likely that the ages of females D E F G H and K range between 13 and 25 years of age for at the time of their importation in 1972 their weights indicated adulthood and their physical characteristics suggested sexual maturity and multiparity. However to avoid the possibility of serious error a very conservative estimation of the ages of these Indian born females based upon an estimated average age of four at first conception is thirteen years. It is likely that these females are in fact many years older.

TABLE 1 Displacement Rank Age Birth Records and Number of Minutes Each Female Was Observed in This Study*

Group 1						Group 2			
Rank over 6 mos	Ss	Age in years	Total births (surviving)	Focal minutes	Rank over 8 mos	Ss	Age in years	Total births (surviving)	Focal minutes
1	A	9	3 (2)	1 050	1	G	> 13	1 (1)	2 380
2	B	7	2 (2)	1 900	2	H	> 13	3 (2)	2 920
3	C	4	1 (0)	1 370	3	I	7	3 (0)	2 930
4	D	> 13	2 (2)	1 080	4	J	7 5	2 (1)	820
5	E	> 13	0 (0)	1 100	5	K	> 13	2 (1)	2 350
6	F	> 13	3 (3)	780					
Total sample minutes 7 780					Total sample minutes 11 390				

* Females are ranked by minimizing the number of times a female is displaced by females ranked beneath her

TABLE IIa Displacement Matrix — Group 1

Rank	Ss	Displaces Ss						Total displacements
		A	B	C	D	E	F	
1	A	—	10	5	12	12	17	56
2	B	7	—	17	11	23	31	89
3	C	4	13	—	12	39	33	101
4	D	2	6	14	—	8	11	41
5	E	4	3	14	8	—	14	43
6	F	3	6	16	5	7	—	37
Total number of times displaced		20	38	66	48	89	106	365

TABLE IIb Displacement matrix — Group 2

Rank	Ss	Displaces Ss					Total displacements
		G	H	I	J	K	
1	G	—	23	60	31	62	176
2	H	7	—	26	15	39	87
3	I	23	18	—	23	71	135
4	J	8	3	2	—	8	21
5	K	5	13	14	4	—	46
Total number of times displaced		53	57	102	73	180	465

RESULTS

Table I presents ranks based upon displacement data with age and the birth records of females of groups 1 and 2. Tables IIa and IIb show the actual displacement matrices. Table III summarizes and compares ranks based upon displacements with ranks based upon age, reproductive history, and percent involvement in displacement activities. A total of 1 830 female female displacements were recorded, and these constituted approximately 50% of the total displacements in which adult females were involved. The other 50% involved females with males or infants. It is very important to note that none of these displacements were observed. An analysis of the data shows the youngest females in each group (C and I) occupied middle displacement ranks, had the poorest birth records, and were engaged in the highest and next to highest frequency of female female dis-

TABLE III Rank Ordering for the Adult Females of Two Groups

Rank	Displacement	Age	Birth records	Involvement
<u>Group 1</u>				
1	A	F D E	F	C
2	B		D B	F
3	C			E
4	D	A	A	B
5	E	B	E	D
6	F	C	C	A
<u>Group 2</u>				
1	G	G H I	K	I
2	H		G H	G
3	I			K
4	J	J	J	H
5	K	I	I	J

Each column represents an order from most to least dominant according to the criterion at the top of the column. Rank one indicates in column 1 most dominant in column 2 oldest in column 3 best birth records and in column 4 most frequent involvement in displacement.

placement activities. The oldest females occupied a range of displacement ranks varying from rank 1 (G) to the lowest ranks in both groups (F and K). Furthermore, as defined by the number of surviving infants produced, the oldest females in each of the groups experienced the greatest success as seen in Table III.

Several interesting difficulties arising from constructing a linear displacement based ranking system demonstrate the unprofitable nature of such a unistrand approach to understanding langur female rank behavior. For example, the data show that among related females A, C, and D, mother D displaced her younger daughter C more often than C displaced her (D), and the oldest daughter A displaced all others most often. Yet, mother D, according to a displacement based system, is ranked under her daughter C because C, a very active displacer, had high frequencies of displacement with females E and F. In other words, because daughter C engaged in more dominance related behaviors with respect to other females, she succeeds her mother's rank position. The mother interacted less frequently than did her daughter but her success rate is much greater. Arranging female displacement ranks linearly obscures the fact that females A, B, C, and females D, E, F form two dominance layers in which statistical significance in frequencies of displacements differs between but not within these subsets. Similarly, for Group 2, dominance layer G, H, and I can be statistically differentiated from layer J, K.

The most accurate diagrammatic representation of female langur rank resembles a layered cake. Inasmuch as no statistical differences in displacement rates separate animal A from B and animal II from C, they share one dominance layer. A student T test at the 0.001 level reveals significant differences between displacement frequencies between C and D, but statistically significant differences do not exist between D, E, and F. Therefore a synthesis of the relationships between these sets of displacement data indicates two major dominance layers — females A, B, and C share one layer, the top one, while females D, E, and F share another — in this case the second or lower of only two layers. More layers have been observed in free ranging troops with a larger number of adult female members [Jay 1963]. As stated earlier, the same statistical differences separate females G, H, and I from J and K in the second group.

Data collected on two females who gave birth during the present study demonstrate that reproductive state does affect rank when it is defined according to displacement data. For example, an analysis of pre- and postparturition data on female G shows that before giving birth she was involved in 1.78 displacement bouts per ten minute focal sample ($n = 1,430$) with all members of her group. With respect only to females, she was involved in an average of 2.15 female-female displacements per focal sample. After giving birth she was involved in significantly less ($\chi^2 < P .001$) or 0.42 female-female displacements. Most importantly, while female G was actively dominant, she succeeded in displacing 2.72 females per sample prior to parturition. The general effect was that while female G occupied top rank in group 2 before giving birth, she shared the top rank with female L after parturition. Similarly, for female B in group 1, there was a noticeable drop in the frequency of her participation in dominant-related activities post-parturition.

The younger primiparous females of the Berkeley colony have high infant mortality rates comparable to the mortality figures presented by Drickamer [1974] for rhesus macaques. Based on birth records of 22 pregnancies during the years when all but one of the adult females conceived since 1974, it appears that reproductive success increases with age. The six oldest females in our colony, for example, although not more fertile, delivered a larger number of viable infants (1 loss of 11 births) than the five youngest females (6 losses of 11 births). Since 1974, when the colony was established, the older females all wild-born have delivered 1 nonviable and 18 viable infants. This is a 5% loss of neonates. The results strongly suggest that langurs do not differ in fecundity rates from rhesus macaques of which up to 45% of first and second born infants of young females die [Drickamer 1974].

DISCUSSION

The interpretation of female langur behavior is currently the subject of major controversy — specifically the relationship between reproductive value and fitness, age, and social rank. Blaffer Hrdy [1977] and others assert that a decline in

reproductive value of female langurs occurs with increasing age and is associated with a corresponding decline in rank. The reproductive value for old females is not only very low but these females no longer vigorously contest dominance with younger females (presumed by Blaffer Hrdy to be kin) because the older females' inclusive fitness benefits are greater if resources are allocated to their younger, presumably more fertile kin. According to this view, age best predicts the direction of rank changes, with younger females rapidly assuming top ranking positions at the expense of the older troop females. Old, low-dominance ranked females are viewed as still fierce in non-dominance contests such as defense of the troop against domestic dogs or the approach of nontroop adult males.

Two assumptions in the above need to be questioned: 1) That old age confers drastically reduced reproductive value, and 2) that old age results in lowered dominance status. According to Blaffer Hrdy and Hrdy [1976: 915], "old females have less to lose from risk taking in terms of future reproduction than do younger animals." An example is given of an old female defending an infant at best her granddaughter, while the infant's mother remains inactive. The mother's inactivity suggests that the benefit to recipient/cost to altruist ratio is very low. The reproductive value risked by the old female is assumed to be very low indeed. Our data from the colony and other data from the field indicate that the reproductive abilities of even quite old females are substantial. It is our contention that few female langurs survive to even close to menopausal age in the rigors of the field and that the estimates of age employed by Blaffer Hrdy are inadequate. For the model proposed by Blaffer Hrdy and Hrdy [1976] to work, it is essential that the older females are really as old as 25, 26, or 27 and that they have ceased to reproduce successfully. As of the present, and in terms of langur data, it has not been shown at what age, if any, langurs experience menopause. If there proves to be subgroups of post-menopausal females in langur troops, then the idea that these females defer to younger females may be understood in the context of fitness models. However, if older females continue to reproduce as successfully as our data would indicate, then there would seem to be few, if any, definite advantages.

Aside from these criticisms, Blaffer Hrdy and Hrdy's contention that differences in reproduction at different ages are due to fecundity differences and not mortality may be questioned because of the intermittent nature of their observations. When behavior is not monitored throughout the year, it is possible to miss births. One may make statements about surviving infants with some reliability, but not about the numbers of infants born.

The second major issue centers on the assertion that old age results in lowered dominance, and once again our data do not indicate that this is the case. The evidence for this is presented in Tables I, II, and III. Clearly, age is not a useful predictor of displacement rank, reproductive success, or degree of involvement in agonistic interactions, except for individuals of very great age, or females who survive to menopausal age. Nowhere is the role of individual personality or temperament

clearer than in dominance behavior but unfortunately both of these variables are hard to measure. Inclination to interact varies tremendously among adult females — from low to high regardless of age. It is not the number of times an animal attempts to dominate as much as the frequency of success that counts in establishing priority of access to desired commodities, animals, or places among the females of the troop. Preferences in association express themselves in dominance interactions with certain females constantly interacting with some but not others in the troop. Adult females do not give preferential treatment to related animals after the latter reach adulthood.

On the basis of five two- to three-month observation periods separated by gaps of up to fourteen months, Blaffer Hrdy maintains that the outcomes of displacement interactions were predictable on a day-to-day basis but not necessarily constant between study periods [1977:165]. This statement is not surprising in view of the long gaps between short observation periods. Data from captive and most field locations indicate that female displacement-based rank fluctuates in concordance with changes in reproductive cycles and the rearing of young. It was possible to predict rank change based upon age for at least two of the Abu troops. Our data, however, permit no such prediction and in fact show that both older and younger females can be found intermixed in ranking order. In addition, irrespective of age, ranks change.

If the captive setting has an effect upon the type of data retrieved, most likely it is an increase in the chances that relatively stable hierarchies among females could be observed and defined. Similarly, the effect might also be to enhance the utility of measuring aggressive displacements to determine rank and ultimately to determine who could reproduce. Rowell [1972] and others have pointed out that reducing space tends to facilitate the emergence of hierarchies but certainly does not tend to diminish them. Yet it is in only a few field locations rather than in the laboratory that data support the construction of linear hierarchies for female langurs. Many field studies of common langurs corroborate our view of rank as minimally important in female day-to-day life [Bogges 1975, Sugiyama 1976, Jay 1963].

SUMMARY

The picture emerging from our colony study of female langur behavior indicates that rank based on displacements is neither correlated with nor best predicted by female age or reproductive value. A composite of factors such as group composition, presence of uterine kin, reproductive state, and individual personality are hypothesized to predict changes in female rank far better than does reproductive value, a concept directly related to female age. There is a positive relationship between increasing age and successful reproduction. The notion of linear ranking is not useful to the understanding of langur female behavior and elucidates

important differences between these Colobine leaf-eating monkeys and the more nepotistic and sometimes dominance-oriented Cercopithecines. For the latter, social rank may correlate with reproductive success [Smuts 1972; Deag 1977; Dickman 1974]. The net result of further exploring the versatile Colobines is to obtain a broader understanding of primate behavior and to secure data that may be used with caution in interpreting the specific and general mechanisms of natural selection and evolutionary change.

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Alterations in Shock-Induced Fighting and Locomotor Activity Following Intracerebroventricular Injection of Hydrocortisone in the Rat

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Three experiments were conducted in an attempt to clarify the facilitatory influence of hydrocortisone on shock-induced fighting in rats. Results of the first experiment indicated a biphasic dose-dependent action of intraventricularly administered hydrocortisone. Low (25 µg) and intermediate (50 µg) doses both facilitated fighting whilst the high (100 µg) dose exerted a potent suppressant effect. Two control tests were performed to determine whether alterations in pain reactivity or locomotor activity could have accounted for the observed changes in fighting behaviour. None of the treatments altered shock thresholds (Experiment 2) but whilst neither low nor intermediate doses affected activity measures, the high dose preferentially reduced vertical activity (Experiment 3).

Key words shock induced fighting activity pain thresholds hydrocortisone rats

INTRODUCTION

Over the past decade considerable experimental evidence has accumulated for pituitary/adrenocortical involvement in agonistic behaviour (Brain 1972 Leshner 1975). Bilateral adrenalectomy reduces isolation induced fighting in mice (Brain et al 1971 Harding and Leshner 1972 Leshner et al 1973) an effect also observed following hypophysectomy (Sigg et al 1966). Corticotrophin (ACTH) acts

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differently on fighting behaviour according to treatment regimen. Chronic administration of ACTH suppresses isolation induced fighting in mice [Brain et al 1971, Brain and Poole 1974, Leshner et al 1973, Poole and Brain 1975a] whilst acute ACTH treatment augments this behaviour [Brain and Evans 1977, Poole and Brain 1975b]. Although the former effect appears to correspond to an extra adrenal action of ACTH, the latter response has been tentatively related to enhanced glucocorticoid release [Brain and Evans 1977]. Glucocorticoid injections (natural and synthetic) have been reported to increase isolation induced fighting [Banerjee 1971, Brain et al 1971, Kostowski et al 1970, Leshner et al 1973] and shock induced fighting [Kostowski 1967] in mice and to restore aggressive behaviour in adrenalectomized mice [Walker and Leshner 1972]. This treatment also increases muricidal behaviour [Kostowski 1967] and maternal aggression [Endroczi et al 1958] in rats. In spite of this wealth of data it has been argued that corticosterone treatment has no effect on murine aggression independent of its effects on ACTH levels [Leshner et al 1973].

In a recent extension of the above research, Rodgers and Semple [1978] reported that shock induced fighting was suppressed by adrenalectomy, hypophysectomy and high doses of ACTH. In contrast, fighting was enhanced by hydrocortisone and low ACTH doses. The present report attempted to investigate the facilitative influence of hydrocortisone on shock induced fighting by using intraventricular injections. This method has the advantage of ensuring that the hormone reaches brain tissue in significant concentrations, thus reducing the possibility of peripherally-mediated behavioural changes. Since the frequency of fighting in this paradigm can easily be influenced indirectly, two control experiments were performed to assess the possibility of treatment induced alterations in locomotor activity and pain reactivity.

GENERAL METHODS

Animals and Surgery

Adult male Sprague Dawley rats (260–300 gm) from Bradford University colony were used as subjects. Animals were individually housed with food and water available *ad libitum* and maintained on a 12 hour light/dark cycle (7 am–7 pm). All testing was performed under red light during the dark phase, i.e. 7 pm onwards.

Under Equithesin anaesthesia (Jensen Salsbery Lab Inc.) experimental animals were implanted unilaterally with guide cannulae terminating 1 mm dorsal to the right lateral ventricle (A/P – 2.0, L 1.8, V 2.0 mm, calculated with reference to Bregma). Cannulae consisted of 23 gauge stainless-steel guides fitted with 31 gauge stylets. The animals received a single intramuscular injection of penicillin

(50 000 units) following surgery and were allowed at least seven days recovery before behavioural testing

Injection Technique and Hormone Doses

During injection stylets were replaced with 31 gauge injection units which extended 1 mm ventral to the guide tip. Single unilateral injections were performed whilst the animals were hand held. A 10 μ l Hamilton microsyringe (model 710N) with a polythene tubing connection to the injection unit was employed to deliver the solutions. Ten μ l injections were made at a rate of 1 μ l/15 seconds with a total injection time of approximately 150 seconds. An uptake time of one hour was adopted in the present study to allow for widespread hormone diffusion throughout the ventricular lumen and adjacent tissue.

Hydrocortisone sodium succinate (Organon NV Oss Holland) was used in three dose levels (25 μ g/10 μ l, 50 μ g/10 μ l, 100 μ g/10 μ l) with injection water serving as both hormone solvent and placebo solution. Each animal received one injection only and was used only once in behavioural testing.

Histology

Prior to sacrifice experimental animals received a unilateral injection of trypan blue dye (10 μ l) into the right lateral ventricle. One hour later animals were given an overdose of Nembutal and perfused intracardially with normal saline followed by 10% formal saline. Brains were removed, hardened in formal saline and sectioned on a freeze microtome. In all but three cases (where data were discarded) dye was observed in maximum concentration around the site of injection (ventriculus lateralis) with widespread distribution noted throughout the ventricular system. Most notably significant staining was seen at the medial portion of the basal hypothalamus in the area of the median eminence. Although these observations do not in any sense quantify hormonal distribution they nevertheless indicate that one hour after unilateral intraventricular injection of a 10 μ l volume significant staining occurs throughout the ventricular system and adjacent tissues.

Apparatus

Shock-induced fighting and flinch jump tests A modified rat operant station (manipulanda removed flat interface) measuring 23.5 X 22 X 22 cm served as the test chamber. The chamber was opaque apart from the perspex door which also served as an observation window. An Aim Bioscience shock generator (Model 507) applied electric shock of specified intensity, duration and frequency to the grid floor of the test chamber.

Activity test A square enclosure with plywood floor (90 X 90 cm) and walls (30 cm high) painted flat white was used. Embedded in two adjacent walls were

two banks of six red light sources. The lower bank was positioned at 3 cm above the floor level (to monitor horizontal activity) with the upper bank at 12.5 cm (to monitor vertical activity). On the opposing walls, two banks of six sensors each were arranged to receive light beams from the corresponding sources. Sensors from lower and upper banks were connected to separate counters which registered one count each time an appropriate light beam was interrupted.

Procedure

Shock induced fighting Operated animals and unoperated stimulus opponents were matched for weight and fighting pairs were randomly assigned to treatment conditions. Pairs were placed in the test chamber one hour after intraventricular hormone or placebo injection to the experimental animal. After two minutes habituation, the animals were exposed to 60 electric shocks delivered to the grid bars (shock intensity 2 mA, duration 0.5 sec, frequency 6/min). An attack response was recorded when one animal made a directed forward lunge either with the forepaws or the whole body. The upright boxing posture itself did not in this study constitute an attack response. Only the behaviour of the injected animals was used in data analysis.

Flinch jump test Pain reactivity was measured using a modification of the flinch jump threshold test (Evans 1961, Rodgers 1977). One hour after either hydrocortisone or placebo injection, individual animals were placed in the test chamber where they received six series of eight electric shocks (0.5 sec duration) delivered at ten second intervals to the grid floor. Shock series were administered in alternating ascending and descending order with intensities ranging between 0.13 and 1.00 mA in eight steps. Jump thresholds (the intensity at which the hind paws leave the grid floor) were recorded for each series and an overall mean value calculated to provide an estimate of pain reactivity.

Activity test One hour following intraventricular treatment, individual animals were placed in the activity box and horizontal activity, vertical activity and defecation scores were recorded over a ten minute observation period.

In all behavioural tests, the apparatus used was cleansed thoroughly after each animal in order to minimize the effects of any olfactory cues from the preceding subjects.

EXPERIMENT 1

This experiment was designed to examine the effect of intraventricular hydrocortisone injection on shock induced fighting. Prior to treatment allocation, 34 operated animals were weight matched with unoperated stimulus opponents. Four treatment conditions were used: placebo (n of pairs = 10), 25 μ g hydrocortisone (n = 8), 50 μ g hydrocortisone (n = 8) and 100 μ g hydrocortisone.

($n = 8$) One hour following injection each pair was placed in the test chamber and the frequency of fighting behaviour was recorded

Results

Results of this experiment are presented in Figure 1. ANOVA revealed an overall significance in attack frequency ($F = 18.4$, F_{999} (3, 30) = 7.05, $P < 0.001$). Statistical follow up using Newman Keuls test for comparison between treatment means indicated that the 25 μg and 50 μg doses of hydrocortisone resulted in significantly increased fighting behaviour ($P < 0.01$) compared with placebo treatment and that the 100 μg dose of hydrocortisone significantly depressed fighting ($P < 0.01$) compared with all the other treatments. It would thus appear that intraventricular hydrocortisone produces a dose-dependent biphasic alteration in shock induced fighting in rats. Casual observation suggested that whilst animals receiving doses of 25 μg or 50 μg initiated and maintained fight encounters those receiving 100 μg doses did not do so and were more actively engaged in overt avoidance and submissive/defensive behaviours.

EXPERIMENT 2

It is well established that alterations in shock sensitivity can indirectly modify levels of fighting in the present test paradigm [Rodgers 1977]. In order to control for this possible explanation of the above results a second experiment was conducted in which shock thresholds were estimated under the treatment conditions employed in Experiment 1. Twenty naive animals equipped with unilateral intraventricular cannulae were randomly assigned to one of four equal treatment

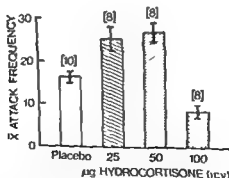


Fig 1 The effects of intraventricular hydrocortisone and placebo injections on attack frequency ($\bar{x} \pm \text{SEM}$) in Experiment 1. Figures in brackets refer to the number of pairs in each condition.

groups (placebo 25 50 and 100 μg hydrocortisone) One hour posttreatment each animal was placed in the test chamber and allowed two minutes habituation before reactivity to electric shock was determined using the flinch jump technique

Results

Results of this experiment are presented in Figure 2 It would seem that hydrocortisone injection at three dose levels does not alter the animal's reactivity to the shock stimulus since ANOVA revealed no overall significance in jump thresholds with treatment ($F = 2.99$ $F_{95}(3, 16) = 3.24$ ns)

EXPERIMENT 3

Another possibility for the results of Experiment 1 is that hormone administration alters motor activity/co-ordination thus indirectly influencing fighting behaviour To test for this possibility 40 naive animals equipped with intraventricular cannulae were randomly assigned to one of four treatment conditions [placebo ($n = 9$) 25 μg ($n = 10$) 50 μg ($n = 10$) 100 μg ($n = 11$) hydrocortisone] One hour following treatment individual animals were placed in the activity box and behaviour was recorded over a ten minute session

Results

Results of this experiment are presented in Figure 3 ANOVA revealed no overall significance either on measures of horizontal activity [$F = 0.82$ $F_{95}(3, 36) = 2.86$ ns] or defecation [$F = 1.81$ $F_{95}(3, 36) = 2.86$ ns] However ANOVA did reveal significance on vertical activity scores [$F = 7.62$ $F_{999}(3, 36) = 6.74$ $P < 0.001$] Statistical follow up using Newman Keuls test indicated

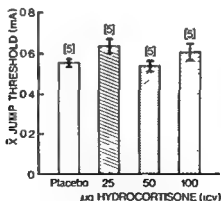


Fig 2 The effects of intraventricular hydrocortisone and placebo injections on shock thresholds ($\bar{x} \pm \text{SEM}$) in Experiment 2 Figures in brackets refer to the number of animals in each condition

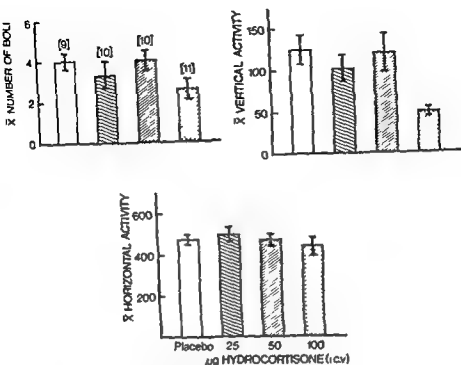


Fig 3 The effects of intraventricular hydrocortisone and placebo injections on three behavioural measures ($\bar{x} \pm \text{SEM}$) in Experiment 3. Figures in brackets refer to the number of animals in each condition.

that the 100 µg dose hydrocortisone significantly depressed vertical activity compared to placebo ($P < 0.01$), 25 µg hydrocortisone ($P < 0.05$) and 50 µg hydrocortisone ($P < 0.01$).

DISCUSSION

The results of the present investigation confirm and extend previous observations that glucocorticoids can modify levels of agonistic behaviour in rodents [Banerjee 1971, Brain et al 1971, Brain and Evans 1977, Endröczy et al 1958, Kostowski 1967, Kostowski et al 1970, Leshner et al 1973, Rodgers and Semple 1978, Walker and Leshner 1972]. Intraventricular injection of both low (25 µg) and intermediate (50 µg) doses of hydrocortisone facilitated shock induced fighting behaviour in the rat whilst a high dose (100 µg) exerted a potent suppressant effect (Experiment 1). In the dose range currently employed hydrocortisone failed to alter shock thresholds, thus eliminating the possibility that the effect on

fighting was indirectly mediated via changes in pain reactivity (Experiment 2). This finding confirms the previous observation that shock thresholds remain unaltered following subcutaneously administered hydrocortisone [Rodgers and Semple 1978]. Whilst neither low nor intermediate doses of steroid altered behaviour in the activity test, the high dose preferentially decreased vertical activity (Experiment 3). Thus the possibility exists that the reduced levels of fighting at the high dose reflect a diminished ability to form the upright posture characteristic of fighting in this test. However, casual observation of these animals in Experiment 1 (see Results) indicated that they were capable of forming the posture but that their behaviour was characterized more by increased avoidance of and submission to the opponent. A similar biphasic relationship has previously been reported in murine aggression following peripheral corticosterone treatment [Candland and Leshner 1974].

Since Erskine and Levine [1973] have reported that complete suppression of pituitary adrenal activity (via implants of hydrocortisone into the median eminence) has little effect on shock induced fighting in this species, it is tentatively suggested that the current positive results may reflect an ACTH independent action of the glucocorticoids on neural mechanisms mediating avoidance and attack. Indeed, the finding that peripherally administered hydrocortisone can restore fighting in hypophysectomized animals to near normal levels (unpublished observations) would seem to support this suggestion. It is of interest to note in this context that McEwen et al [1970] have found that cells within the limbic system (including areas traditionally associated with avoidance and attack) selectively accumulate glucocorticoids.

The potentiation of attack produced by both low and intermediate doses of hydrocortisone would appear to contradict the recent suggestion that glucocorticoids are selectively involved in mediating avoidance of attack [Moyer and Leshner 1976; Hock and Leshner 1976]. However, it should be emphasized that the present paradigm differs from that of Leshner's group in several important respects: species (rats vs mice), schedule and route of injection (acute intraventricular vs chronic subcutaneous) and steroid preparation (hydrocortisone vs corticosterone). These methodological differences make a direct comparison of findings difficult. We are currently investigating the effects of chronic vs acute intraventricular injections of glucocorticoids (hydrocortisone and corticosterone) on levels of shock induced fighting.

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Mousekilling, Intermale Fighting, and Conditioned Emotional Response in Rats

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Several possible relationships between two forms of aggression in rats were studied. First, mouse killing and spontaneous intermale fighting were found to be correlated. Rats which attacked other rats were those most likely to kill mice. To determine whether aggressive and nonaggressive rats were also differentially responsive to other situations involving emotional arousal but not aggression, mouse killers and nonkillers were compared in a conditioned emotional response (CER) situation. Mouse killers showed greater suppression to the conditioned stimulus (CS) and to the situational cues of the apparatus. Therefore, a common arousal mechanism may underlie a number of diverse agonistic responses. Nevertheless, extensive mouse killing experience did not increase the tendency of rats to fight with either adult males or juvenile males.

Key words: rat, mouse killing, conditioned emotional response, interspecies aggression, intermale fighting.

INTRODUCTION

Classes or types of aggression (eg, predatory, intermale, irritable) are commonly distinguished either on the basis of their response topography (Clemente et al, 1973) or by the stimulus situation in which they occur (Moyer, 1968). There is

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also ample evidence that different forms of aggression have different physiologic substrates (see reviews by Clemente et al [1973] and by Moyer [1968]). However such categories should not obscure possible relationships between forms of aggression. First the same general laws may apply to each. For example familiarity with the stimulus object inhibits instances of predation [Galef 1970a], irritable aggression [Galef 1970b], and intermale fighting [Marler 1976]. Second there may be intrasubject correlations. A rat which fights frequently in response to shock might also show high levels of spontaneous intermale fighting or mouse killing. Finally experience making one type of aggressive response may facilitate other forms of aggression. The presence of such relationships would suggest that some common mechanisms underlie different aggressive responses.

The experiments reported here examined these three types of possible relationships by comparing mouse killing and intermale fighting in rats. Mouse killing is usually classified as predatory aggression (see review by O Boyle [1974]). Predatory attack is evoked by the presence of an appropriate prey object and usually results in the prey's death. It is considered to be quite different from intermale fighting [Moyer 1968] which is evoked by the presence of a conspecific and involves high arousal and seldom results in the death of either combatant. However at least two manipulations which effect mouse killing have similar effects on intermale fighting. Prior familiarity with the appropriate stimulus animal inhibits both intermale fighting [Galef 1970a] and mouse killing [Galef 1970a] while familiarity with the test environment facilitates both [Barnett 1969, Karl 1956]. In addition food deprivation increases the probability of mouse killing [Paul et al 1971] and may increase fighting between male rats [Davis 1933].

The similarity in conditions which initiate these two kinds of aggression suggest that a common mechanism is involved in both. If so the two behaviors should also be correlated. That is animals that are mouse killers should also be the most vigorous intermale fighters. Experiment 1 therefore examined whether this correlation exists.

GENERAL METHOD

Subjects

Male Long Evans rats weighing 200–300 gm were used as subjects. They were housed and tested in individual wire mesh cages.

Stimulus Animals

Adult male Sprague Dawley rats matched for weight to that of the subject with which each was paired were used in the intermale fighting tests. The juvenile rats used in the fighting tests in experiment 2 weighed 60–120 gm. Adult Swiss mice were used in the mouse killing tests.

Aggression Tests

To test for mouse killing a mouse was placed in the subject's cage for 30 minutes or removed within 60 seconds of death. The latency to kill was recorded.

Tests with the strange male rat lasted 15 minutes. Subjects were rated a) as savage fighters if posttest examination showed that the albino bled from at least one wound, b) as fighters if bites were sufficiently hard to evoke squealing from the victim, or c) as nonfighters if these behaviors were not observed.

EXPERIMENT 1

Method

After one week of ad lib feeding, each of the 75 subjects was maintained at 85% of its ad lib feeding weight. After four days at 85% of its ad lib feeding weight, after four days at 85% body weight, the subjects were tested in counterbalanced order on two days: once with mice and once with male rats.

Results

Twenty-four of the 75 subjects (32%) killed mice, and 17 of the 75 subjects (23%) attacked the strange albino rats. Table I shows that more mouse killers fought other rats than did nonkillers ($\chi^2 = 8.95$, $df = 1$, $P < 0.005$). Furthermore, for rats which killed mice, fighters tended to attack mice more quickly than did nonfighters (median latencies of 60 vs 90 seconds, Mann-Whitney $U = 41$, $df = 11/13$, $P < 0.10$).

Prior exposure to the albino rat had no effect on subsequent mouse killing ($\chi^2 < 1$) and exposure to mice had no appreciable effect on fighting ($\chi^2 = 1.09$, $df = 1$, $P > 0.20$).

EXPERIMENT II

Practice in one kind of aggression may strengthen the tendency to another kind of aggression. Previous aggressive experience can strengthen subsequent

TABLE I. Number and Percentage of Killers and Nonkillers That Fought With an Unfamiliar Male Rat

Response	Type of subject	
	Killer	Nonkiller
Savage fight	2/24 (8.3%)	0/51 (0.0%)
Fight	9/24 (37.5%)	6/51 (11.7%)
No fight	13/24 (54.2%)	45/51 (88.3%)

aggression of the same type [Ginsburg et al 1942 Scott et al 1951] and it can raise the probability of attacking a stimulus animal not ordinarily attacked [Kahn 1951 Lagerspetz et al 1967] Extensive mouse killing experience may increase the percentage of subjects attacking male rats The subjects were tested with both adult and juvenile rats since mouse killing experience does transfer to killing weanling rat pups [Paul et al 1973] A food satiated group was also included to determine if hunger increases fighting Previous studies have obtained conflicting findings [Davis 1933 Lester et al 1968]

Method

Fifty seven subjects were randomly assigned to three groups Then all subjects except those in the Food Satiated group which remained on adlib food were reduced to and maintained at 80% of their adlib weight

After four days at 80% weight the Mouse Exposure group was given 20 mouse killing tests two per day for ten days The two other groups were not tested for mouse killing All three groups were tested for intermale fighting on the two days following the Mouse Exposure group's last mouse killing test By a random method half of the subjects in each group were first tested with a juvenile rat and half were first tested with a mature rat

Results

Although 88% (15/17) of the Mouse Exposure group eventually killed mice this group did not fight more frequently with either adult males ($\chi^2 < 1$) or with juvenile male rats ($\chi^2 < 1$) than did the group not exposed to mice However food-deprived rats (Mouse Exposure and No Mouse Exposure groups combined) were more likely to fight with mature rats ($\chi^2 = 5.21$ $df = 1$ $P < 0.05$) and juvenile rats ($\chi^2 = 3.69$ $df = 1$ $P < 0.10$) than were rats in the Food Satiated group

EXPERIMENT 3

All rats possess the neural mechanisms necessary for mouse killing [King et al 1968 Vogel et al 1971] The difference between those which attack and those which do not must be in how easily the attack can be evoked This difference in aggressiveness may be caused by the killer rats being generally more emotionally responsive If so it should be possible to predict which rats will kill mice on the basis of their emotional responsiveness

In order to attribute such a correlation to general emotional responsiveness the test of emotionality should be quite different from the aggression test Attack involves detection approach and initiation of a sustained pattern of responding to the stimulus animal To eliminate factors governing responsiveness to social stimuli emotionality was assessed by the amount of shock produced disruption

of an ongoing instrumental response (conditioned emotional response CER) CER measures the animal's emotional response to an aversive stimulus [Estes et al 1941]

To insure the reliability of the findings the experiment was replicated with some modifications in procedure

Method

Ten operant chambers were equipped with a stainless steel grid floor a solenoid operated water dipper and a single bar A flashing light stimulus was produced by a 7.5 watt light behind a frosted glass and electric grid shock was produced by a variable transformer and a fixed series resistor The procedure was run in two replications

Replication 1 Eighteen subjects were given food adlib but were water-deprived for 27 hours prior to each experimental session Lever pressing was conditioned for water reinforcement on four sessions of 60 responses each For the remainder of the experiment lever pressing was reinforced on a 60 second variable interval (VI) schedule Daily session length was 90 minutes

Starting on the tenth day of VI training four presentations of a four minute flashing light were given per session After three days of habituation to the light shock was introduced (fear acquisition phase) To maximize individual differences in shock produced suppression shock randomly followed the flashing light (CS) on 50% of the trials On appropriate trials shock onset preceded termination of the CS by 0.5 seconds and terminated 0.5 seconds after the offset of the CS Shock intensity was 0.55 mA for the first four days of fear conditioning and 0.63 mA for the remaining five days Fear acquisition was followed by seven days of fear extinction during which the CS was presented but no shocks delivered The number of responses made each day during the four minute pre CS and 4 minute CS periods were recorded

After the last extinction session all subjects were given free access to water and placed on a 23 hour food-deprivation schedule On the sixth and seventh days subjects were tested for mouse killing

Replication 2 Twenty subjects were subjected to the same procedure as in replication 1 except that the fear acquisition phase lasted 11 days and no extinction phase was run During fear acquisition the shock level on days 1-3 was 0.3 mA on days 4-5 it was 0.4 mA on days 6-7 it was 0.5 mA and on days 8-11 it was 0.65 mA

Results

Replication 1 Eight of the 18 subjects killed mice killers and nonkillers did not differ in their response rates on the last day of VI pretraining (34 vs 58

responses per four minutes Mann Whitney $U = 29$ $P > 0.10$) or during the CS and pre CS periods of the last day of CS habituation (62.4 vs 54.3 $U = 37$ $P > 0.10$ 67.1 vs 66.3 $U = 34$ $P > 0.10$)

Figure 1 shows for killers and nonkillers the daily means of the median (for each subject) number of responses in the CS period of acquisition. Killers were more suppressed during the CS than were nonkillers on the last five days of fear acquisition (3.5 vs 17.9 $U = 11.5$ $P < 0.02$). The mean of the median number of responses for killers and nonkillers during the pre CS interval is shown in Figure 2. Killers were much more suppressed by fear during the pre-CS interval than were nonkillers during the last five days of fear acquisition (19.7 vs 51.7 $U = 9$ $P < 0.01$)

Kamin suppression ratios ($B/(B + A)$ where B is the press rate during the CS and A is the press rate during the four minute period preceding the CS) were

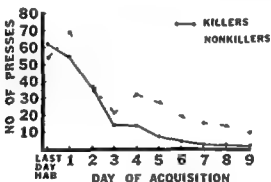


Fig 1 Mean of the median number of presses per day during the CS period for killers and nonkillers

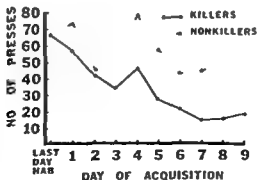


Fig 2 Mean of the median number of presses per day during the pre-CS period for killers and nonkillers

calculated for each session. The median suppression ratio of killers (0.08) on the last five days of acquisition was not reliably different from that (0.21) of non killers ($U = 24$ $P > 0.05$). However, it was reliably lower (0.15 vs 0.34 $U = 13$ $P < 0.02$) on the last two days of fear extinction.

Replication 2 Twelve of the 20 subjects killed mice. Killers and nonkillers did not differ either in their press rate during the last day of VI pretraining (33 vs 42 responses per four minutes $U = 39$ $P > 0.10$) or during the CS and pre-CS periods of the last day of CS habituation (187 vs 253 responses per day $U = 36$ $P > 0.10$, 186 vs 278 responses per day $U = 36$ $P > 0.10$).

On the last five days of fear acquisition the response rate of killers was more suppressed than was that of nonkillers during the pre-CS period (mean of the median number of presses per day 125 vs 309 $U = 17$ $P < 0.02$) but not during the CS period (59 vs 75 $U = 51.5$ $P > 0.10$).

DISCUSSION

The results suggest that two forms of aggression previously considered to be quite distinct probably share a common arousal mechanism. Subjects that fought other rats were also the animals that killed mice. In addition, the mouse killing latencies of rats which attacked strange rats tended to be shorter than those of rats that did not. Nevertheless, experience in mouse killing did not strengthen the tendency to attack novel rats (experiments 1 and 2).

The correlation between mouse killing and CER suggests that aggressive rats are more emotionally responsive and more fearful than are less aggressive rats. Since the subjects were not tested for mouse killing until after the CER tests, factors such as killing experience and food deprivation, which affect the probability of killing, could not have affected CER performance. While mouse killers tended to show greater response suppression than did nonkillers during the CS periods, the greatest difference between these groups was in the amount of suppression during the pre-CS periods of shock acquisition. Two previous studies [Tapp 1964, Weiss et al. 1969] also found that the largest differences in suppression occurred during the pre-CS intervals. Suppression during the pre-CS interval indicates that killers are more emotionally responsive to general situational cues rather than being more easily or strongly conditionable, as would be suggested by differences in responding during the CS periods or by differences in Kamin ratios. This conclusion is supported by Vergnes, Boehrer, and Karli's report [1974] that mouse killing rats were more emotional in an open field situation than were other rats.

Finally, because the response rates of killers and nonkillers were virtually identical prior to fear conditioning, the differences in suppression cannot be attributed to a difference in general activity level. Indeed, these data show that mouse killers and nonkillers are not differentially responsive to all situations.

Differences appeared only when the animals were emotionally aroused either when confronted with a strange rat or in a fear producing situation

Environmental conditions which raise responsiveness presumably via emotional arousal including novelty [Galef 1970a] pain [Bowers 1973 Ulrich et al 1962] and hunger (experiment 2 and Paul et al [1971]) produce increases in both fighting and mouse killing. The data from correlations between mouse killing and fighting and from environmental manipulations support the idea of a common arousal mechanism being involved in several kinds of aggressiveness and fearfulness. Such a commonality would underlie the initiation of the response in these situations. Therefore strengthening one aggressive response might not have any effect on other aggressive responses. This was demonstrated in experiment 2 by the fact that extensive practice in mouse killing did not facilitate intermale fighting. It also explains why mouse killing does not correlate with traditional measures of dominance between rats [Baenninger et al 1970 Barr et al 1975]. Aggressive responses are under multiple control. These experiments suggest the need for research which separates the stimulus and response factors.

These data point to a new criterion for distinguishing between classes of aggression. Previous ways of categorizing leave open some possible relationships such as the demonstrated correlation across animals. Although these data and other considerations (see for example Johnson [1972] p. 20) blur the distinction between categories of aggression it may be useful particularly from a heuristic point of view to keep the distinctions but sharpen the criteria. A good criterion for distinguishing between classes of aggression is nontransfer of the effect of practice from one form of aggression to another.

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Pre-Breeding Aggression in Male and Female Three-Spined Sticklebacks (*Gasterosteus aculeatus*)

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The reactions of 34 female and 32 male three-spined sticklebacks to a conspecific were observed in the month before the breeding season. Factor analysis indicated that the organisation of the response in the two sexes was very similar in both cases; axes labelled "aggression", "threat", "lunosity" and "sex" emerged with male fish having significant ly higher scores on the first factor and females on the second. Any theory of the causes of aggression in sticklebacks should accommodate these facts.

Key words: aggression female male season sexual behaviour stickleback

INTRODUCTION

The traditional picture of aggression in the three spined stickleback is of a behaviour pattern shown by breeding adult males only in defense of a territory and in response to a highly specific stimulus — the red breast of an intruding male [Tinbergen 1951]. However immature sticklebacks of both sexes [Sevenster and Goyens 1975] nonbreeding adults [Huntingford unpublished data] and sexually mature females [Morris 1958 Wootten 1976] also attack conspecifics and not usually in a territorial context. Moreover this response can be elicited by stimuli other than

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breeding males or models of them [Muckensturm 1967 Sevenster and Goyens 1975] In two other species of stickleback (*Pygosteus pungitius* and *Culea inconstans*) females as well as males have been described as territorial in some laboratory studies at least [Hall 1956 Morris 1958] Thus as Wootton [1976] points out a complete understanding of the incidence of aggression in sticklebacks cannot be achieved by studying the behaviour of sexually mature males alone

This paper describes the behaviour of adult male and female three spined sticklebacks observed during a one month period immediately before the onset of the breeding season Although the primary aim of these experiments was an investigation of possible hormonal bases of aggression not necessarily in a territorial context they might also be expected to throw light on more general aspects of the organisation of this behaviour in both sexes

MATERIALS AND METHODS

The observations were carried out on sticklebacks from Inverleith pond Edinburgh in late May and early June of 1977 a year in which the very cold winter and spring delayed the onset of the breeding season All fish were sufficiently large to be capable of breeding (mean weight for males 0.89 gm for females 0.92 gm) but none had reached full reproductive condition

The fish were kept at a temperature of approximately 20 °C on a lighting schedule of 16 hours light—8 hours dark and were fed daily on Tubifex worms and Daphnia They were housed singly in tanks of 60 X 30 X 30 cm for a period of five days before testing which involved placing an adult male with no trace of breeding colours (the stimulus fish) in the centre of the tank confined in the bulb of a glass flask Five minutes observation began when the fish being watched (the test fish) was first in a position from which it could potentially see the stimulus fish During each trial the following behaviour patterns on the part of the test fish were recorded

Facing test fish still with the whole body pointed towards the stimulus fish
This category is subdivided on the basis of whether the test fish is more or less than 10 cm from the stimulus fish

Spine raising complete raising of the dorsal and/or ventral spines

Approach slow movement from a facing position towards the stimulus fish through at least 2 cm starting from a distance of at least 5 cm and not ending in contact with the glass

Lunge rapid dart towards the stimulus fish from a facing position at less than 5 cm and with the mouth closed ending against the glass

Bite rapid jab at the glass flask with the mouth open and then closed

Head-down vertical posture with the side or ventral surface towards the stimulus fish with one or both of the ventral spines raised accompanied by rapid jabbing movements at the substrate

Zig zags one complete towards and away movement with spines raised typical of the male stickleback's courtship dance

After testing the fish were killed for histological investigations and their sex determined altogether 34 females and 32 males were tested

Although these observations were made in an experimental situation traditionally used for studying territorial behaviour (ie an intruder is placed in a tank containing a resident fish) and although at this stage of the year the male fish may have been beginning to establish territories [Van den Assem 1967] this study did not address itself to the question of whether the behaviour observed was site dependent and therefore possibly territorial. The aim was simply to provide a quantitative account of the behaviour patterns shown towards a conspecific by prebreeding fish and to study the temporal relationships of these patterns. Any similarity or lack of it with the obviously territorial response of breeding male sticklebacks is a matter for discussion

RESULTS

Table I shows the mean values for males and females of various measures of the response to the intruder and the results of t tests carried out on the individual scores. Males show significantly higher levels than females for lunges and bites the reverse being the case for head-down threat postures.

In order to investigate more fully the integration of these various acts in the two sexes the scores for all the males and those for all the females were analyzed by the method of principal components followed by Varimax rotation. This method is widely used in psychology and in many branches of biology and its application

TABLE I Mean Values of Eleven Measures of the Response of Male and Female Fish to an Intruder

	Males	Females	t test result
Facing from < 10 cm-No	9.94	9.41	no sig diff
Facing from < 10 cm duration	48.72	43.68	
Facing from > 10 cm-No	2.03	2.23	
Facing from > 10 cm-duration	1.09	4.35	
Spine raising-No	15.25	15.91	
Spine raising-duration	17.46	20.21	
Approaches-No	4.00	4.50	
Lunges-No	176.78	130.18	P < 0.05
Bites-No	98.62	58.09	P < 0.05
Head-down postures-No	1.46	3.47	P < 0.05
Zig zags-No	3.87	2.15	no sig diff

to the territorial behaviour of breeding male sticklebacks is described by Huntingford [1976]. Briefly the analysis investigates the matrix of covariances or correlations between a number of variables (in this case the behaviour patterns shown by the sticklebacks) and produces a new set of axes or factors in terms of which the information contained in the original block of data can be restated. Each factor is characterized by a set of loadings for all of the original variables with those variables which are correlated loading on the same factor and those which are unrelated loading on different ones. Thus in the present case groups of causally related behaviour patterns can be identified in an objective way on the basis of the fact that they all have high loadings on a given factor. In addition a compound measure (referred to here as the factor score) reflecting the overall performance of an individual subject with respect to a particular group of behaviour patterns can be calculated from the loadings of each behaviour pattern on the relevant factor and the fish's original scores for these variables. Thus this method of analysis provides a picture of the overall response to the stimulus fish in sticklebacks of both sexes and a method of quantifying the behavioural differences between individual fish.

Figure 1 shows the first four factors to emerge from the two analyses. These not only account for an identical proportion (81%) of the total variance but also

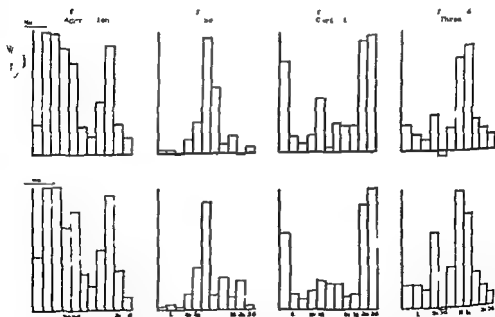


FIG. 1. Structure of the first four factors which emerged from analyses of data from prebreeding males and females. Vertical axis: size of factor loading for each variable on an arbitrary scale. Horizontal axis: behaviour patterns used in analyses. Key to variables: A—approach; L—lunge; B—bites; Sn and Sd—number and duration of spine raising; Z—zig; H—head-down; In and Id—number and duration of facing from less than 10 cm; Zn and Zd—number and duration of facing from more than 10 cm.

have remarkably similar patterns of loadings in the two sexes. Factor a which has high loadings for lunges, bites and facing from close up provides an index of overt aggression, distinct from factor d whose high loadings for head down threat and facing indicate a dimension of threat independent of actual attack. Factor c with high loadings for lunges, bites, spine raising and facing from close up provides an index of overt aggression, as distinct from factor d whose high loadings for head down threat and facing indicate a dimension of threat independent of actual attack. Factor c with high loadings for approach and facing from a distance represents what might be called 'curiosity' on the part of the sticklebacks while factor b reflects the sexual aspect of the response having high loading for zig zags. Thus the analysis has identified four major dimensions in the response of both prebreeding males and prebreeding females to a conspecific introduced into a familiar tank.

Table II shows the mean scores of the two sexes on these four factors and the results of *t* tests on the scores of the individual fish. There are no significant differences between the scores of males and females on factors b or c but as might be expected from the raw data, males have significantly higher scores on the aggression axis (a) and females on the threat axis (d).

DISCUSSION

a. Factor Structure

Multivariate analysis of the data obtained from these prebreeding sticklebacks has identified dimensions in the behaviour of both sexes which have been referred to as overt aggression, threat, curiosity and sexual behaviour. This marked similarity in the structure of the four major factors in male and female prebreeding fish indicates that the organisation of the response to the stimulus fish in the two sexes is alike. Where the first three factors are concerned this was perhaps to be expected since, as already mentioned, female sticklebacks are known to approach, investigate, threaten and attack conspecifics [Wootton 1976] to quote Morris [1958] 'The aggressive actions and postures occur in both sexes (of *Pygosteus*) in exactly the same way'. A partial explanation in physiological terms for this similarity of behavioural organisation may lie in the fact that the level of aggression

TABLE II. Mean Scores of Males and Females on Factors a-d

	Males	Females	<i>t</i> test result
Factor a (aggression)	0.94	0.60	$P = 0.05$
Factor b (sex)	-0.17	-1.60	no sig diff
Factor c (curiosity)	0.17	0.53	no sig diff
Factor d (threat)	0.23	0.91	$P < 0.05$

shown by sticklebacks appears to be partly controlled by gonadotropic hormones [Baggerman 1956 Hoar 1962 Wootton 1970]. Both males and females in these experiments had well developed but not fully developed gonads. They therefore presumably had the high levels of circulating gonadotropins necessary for aggressive behaviour to rise towards the high levels associated with breeding in the males. However, this observation pushes the question one stage back since it is now necessary to assume that the neural substrates on which the gonadotropins act to produce aggressive behaviour are similar in organisation in the two sexes; this need not necessarily have been the case.

On the other hand, the fact that females showed the zig zagging movements usually thought of as typical of the courting male stickleback is more difficult to understand. In both sexes, bouts of zig zagging were relatively rare and of short duration compared with those shown by fully breeding males; however, the zig zagging movements that the females did perform were indistinguishable from those of the prebreeding male fish. There is no possibility that the sexes were wrongly assigned as all the females had well developed ovaries and there was no indication from the state of their kidney tubules that these fish were producing any testosterone [Hoar 1962], a hormone which is known to be involved in the sexual behaviour of sticklebacks [Wai and Hoar 1963]. Morris [1952] has described the occurrence of 'pseudo female' behaviour in male sticklebacks, although his interpretation has been questioned [Van den Assem 1967]. He gives no examples of 'pseudo male' behaviour of females of this species, although he does point out that where one sex performs the patterns belonging to another sex it is more frequently the female that performs the male pattern rather than vice versa. Otherwise the male behaviour shown by the females in this experiment was completely unexpected and its significance is unclear. It is possible that as Tinbergen suggested four scores used in particular in the ways of measuring the amount of facing from the two distances (see legends of Figs 1 and 2). In spite of these facts, recogni-

In order to allow some comparison of the behaviour of these prebreeding sticklebacks with that shown by breeding fish, Figure 2 reproduces the results of a Principal Components Analysis with Varimax rotation on some data collected from breeding males with newly built nests [Huntingford 1976]. There are obviously physiological differences between these two sets of fish, as well as a difference in their immediate environment. In addition, the stimulus fish used was a male in full breeding colours and there were some minor differences in the actual behaviour scores used in particular in the ways of measuring the amount of facing from the two distances (see legends of Figs 1 and 2). In spite of these facts, recognizable dimensions of aggression, curiosity and sexual behaviour emerge in both cases. Thus, it would appear that the structure of the response to the stimulus fish in prebreeding sticklebacks of both sexes is broadly similar to that of the more commonly studied fully reproductive males towards a territorial intruder. However, there are two obvious differences. In the first place, no axis of nest activity emerged from the present data, which is hardly surprising since none of the subjects built nests. Secondly, there is no equivalent of the prebreeding factor II in the earlier studies of

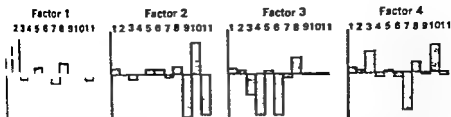


Fig 2 Structure of first four factors which emerged from analysis of data from fully breeding males [Huntingford 1976] Vertical axis size of factor loading for each variable on an arbitrary scale Horizontal axis behaviour patterns used in analysis. Key to variables 1 number of lunges 2 number of bites 3 number of zig zags 4 number of bouts of nest activity 5 number of spine rasure incidents 6 total duration of nest activity 7 total duration of spine rasure 8 9 mean bout length of facing from less than 10 and more than 20 cm 10 11 proportion of time facing from less than 10 and more than 20 cm Factor 1 = "aggression" Factor 2 = "territory" Factor 3 = "nest activity" Factor 4 = "sexual behaviour"

fully breeding males. This is because head-down threats were extremely rare in those experiments a fact which is less easy to explain. Tinbergen [1952] suggested that head-down threats in sticklebacks is derived from a displacement activity resulting from a conflict between the tendency to attack and to flee thus accounting for their occurrence mainly at territorial boundaries. Bearing this in mind there are at least two possible explanations for the absence of head-down threats in the 1976 tests. The first is based on another (unintentional) difference in experimental technique between the two sets of tests. It is generally accepted that a member of a territorial species placed in the territory of a conspecific invariably flees from the resident's attack. In the 1976 experiments this always happened. However in the present experiments the stimulus fish often counterattacked either because sticklebacks from Inverleith pond are particularly aggressive (Huntingford unpublished data) or because test fish without full breeding colours are less intimidating or both. As head-down threat was often shown in response to this unusual situation it is possible that the motivational conditions which produce the display were provided in the present experiments but not in earlier studies. Alternatively the difference in frequency of performance of head-down threat may represent a real difference in the response of prebreeding and fully breeding sticklebacks to the experimental situation. For example in the absence of a well defined territorial system as in the prebreeding tests conflict between attacking and fleeing in reaction to a stimulus fish may occur more often. These two possibilities are not mutually exclusive.

b. Scores of Individual Fish

Although the males have significantly higher scores on the aggression factor the female sticklebacks still showed well developed aggression in these tests. The fact that females have higher threat scores may reflect their lower aggressiveness as well as a possible difference in fearfulness making the motivational balance be responsible for this posture more often achieved in this sex.

CONCLUSIONS

The results described above indicate that the organisation of the responses of male and female three spined sticklebacks to a strange conspecific in the period just before the breeding season are broadly similar as are the responses of pre breeding and fully breeding males although the actual levels of the behaviour pattern may differ. Any theory of the control of aggression in sticklebacks must take this into account.

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Aggressiveness and Dominance in Captive Cock Red Grouse

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A method for measuring the aggressiveness of captive cock red grouse is described. A cock's aggressiveness varied according to season, type of cage and social environment. A method for ranking the dominance order of cocks in a group is also described. Dominance ranks remained stable for up to two years. Correlations between the aggressiveness of isolated cocks and their dominance ranks when in a group were positive but weak. Aggressiveness and dominance should be clearly distinguished. Both aggressiveness and dominance were related to the size of cock's combs and implants of testosterone increased all three. In situations where a cock's aggressiveness changed, comb size changed in the same direction. The aggressive behaviour of captive cocks shows several major parallels with that of wild cocks.

Key words: aggression dominance comb size red grouse courtship

INTRODUCTION

In wild red grouse (*Lagopus lagopus scoticus*) territory size is correlated with aggressive behaviour and changes in aggressive behaviour are followed by inverse

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changes in population density [Watson and Moss 1972]. The aim of the present study was to measure aggressiveness and dominance in captive cock grouse to help improve our understanding of population change in the wild.

Aggression is a term which has been used in so many ways by different workers [Brain 1977] that we have avoided it. In this paper we use dominance to mean that social relationship which indicates the usual direction of aggressive acts between animals. The frequency or intensity of such acts, which we call aggressiveness, is not necessarily related to their direction. We therefore measured dominance and aggressiveness separately.

HUSBANDRY

Captive birds were hatched in captivity from eggs collected in the wild and from eggs laid in captivity. Moss [1969] describes incubation, rearing and husbandry.

Chicks were reared in brooder houses measuring 1.2 m X 1.2 m attached to 3 m X 3 m runs; all groups were of 20–25 until 12 weeks of age when they were moved to cages 2.5 m X 1.2 m X 0.9 m in size with 8 birds to a cage. In October or November we measured the aggressiveness of each cock in a separate isolation cage (0.85 m X 0.90 m) where it could hear but not see other cocks. Afterwards dominance was tested in larger cages (1.2 m X 2.4 m) and other tests were done subsequently in other large cages. When not being tested, cocks were in the isolation cages or in the larger cages with hens.

AGGRESSIVENESS

Hinde [1970] defined aggression as behaviour in which an animal attacks or threatens a conspecific in order to displace it, and Huntingford [1976] noted that inter- and intraspecific aggression are often closely linked. We developed an aggressiveness score based on calls, threats and attacks towards a human observer as this was the easiest way to elicit aggressive behaviour from captive cocks. To justify the relevance of this to intraspecific encounters, we checked (below) that a cock's tendencies to call at, threaten or attack a human observer and another cock grouse were correlated.

In this paper we describe several methods for measuring aggressiveness including nominal classification, scoring and ranking. Nominal classification of calls and acts (Tables I–II, Appendix) was a necessary preliminary to scoring. However, after the aggressiveness score had been justified, we used it for all measure-

TABLE I. Number of Cock Red Grouse Which Threatened or Attacked an Observer Standing in Front of Each Cage in Relation to the Calls That Each Cock Gave During One 10-Second Observation in February

kind of call	No threat or attack	Threat	Attack	Statistical comparison between lines	Significance level
No a b or c	58	0	0	1 vs 2 ^a	0.05
a only	23	2	1	2 vs 3 and 4 combined ^a	0.005
a & b	4	5	3		
a, b & c b & c or a & c	3	1	5	3 vs 4 ^b	0.136

^a 2 X 2 contingency table, combining threat and attack

^b Fisher exact probability

This (February) result was typical of hundreds of sets of observations when scoring cocks for aggressiveness except that a large sample was used here for statistical reasons

TABLE II. Response of 51 Red Grouse Cocks to a Human and a Stuffed Grouse (April) During One 10-Second Observation

Response to stuffed grouse	Response to human				
	escape	none	call a	calls b or c with or without a	attack/threat
escape	1	4	2	1	1
none	0	14	7	3	2
call a	0	0	4	0	1
call b or c	0	0	1	1	1
attack/threat	0	0	0	0	5

Responses are ordered from escape (taking flight or running up and down the back of the cage) to most aggressive (attack/threat). The contingency coefficient *C* (with five degrees of freedom) was calculated by classifying responses to stuffed grouse as: 1) the same as the response to a human; 2) one category more aggressive or less aggressive; 3) two categories different; 4) three categories different; 5) four categories different ($C = 0.63$, $P < 0.001$).

ments where cocks were held long enough (a week or more) to allow the repeated observations necessary for it. When measurements had to be made over too short a period to allow this, aggressiveness was ranked.

Calls, Postures and Acts of Threat and Attack

Watson and Jenkins [1964] described several postures and associated calls that wild cocks use whilst excluding other cocks from their territories. Caged cocks also show these towards other cocks and towards human observers. We noted the occurrence of three of these calls, the appropriate phonetics by Watson and Jenkins [1964] being

krow for our call a which they associated with threat

kohway for our b which they associated with attack intention and

kohwah for our c which they associated with attack.

We avoided making assumptions about the meaning of different postures by recording attack only when a cock tried to peck or buffet the observer through the wires and threat when it called and advanced to the front of the cage but did not touch the wires. Birds calling but not advancing were recorded as mere giving calls a, b or c.

Some cocks called, threatened and attacked more than others, which suggests that these cocks were being more aggressive. To check this we noted whether calls a, b and c accompanied threat and attack in captive cocks, as in wild cocks [Watson and Jenkins 1964]. An observer to whom the birds were accustomed spent ten-second periods standing in front of each cock in its isolation cage, noting separately each type of call made by the bird, and also whether or not it attacked or threatened him.

Cocks giving call a only were more likely to threaten or attack the observer than those not calling at all, but were less likely to do so than those giving some b and/or c (Table 1). Although cocks that gave some c calls attacked the observer more often than those that gave a and b but no c, this difference was not significant. We concluded that calls a, b and c accompanied aggressive responses to an observer, and b and c accompanied a more aggressive response than a on its own.

Scoring of Aggressiveness

To score the aggressiveness of each cock, an observer walked along a row of cages, paused for ten seconds in front of each, and recorded whether that cock gave calls a, b or c, and whether it threatened or attacked him. He did this twice a day for seven to ten days. He gave 2 points if a cock called and attacked (no cock attacked without calling), 1½ if it advanced towards him and called with

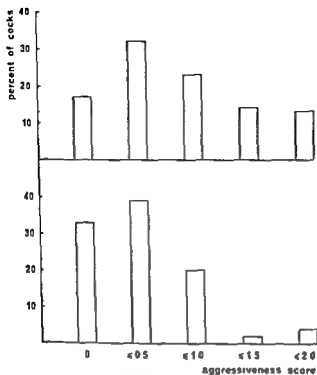


Fig 1 Distribution of aggressiveness scores in March (top 69 cocks) and November (bottom 51 cocks)

out attacking, 1 if it called when he stood in front of it and $\frac{1}{2}$ if it called only when he was approaching or leaving. To calculate an individual cock's aggressiveness score we divided the total number of points for that cock by the number of ten-second observations for it (see Appendix for a detailed justification).

Although the aggressiveness score was a parametric measure it was not normally distributed (Fig 1) and so it may not be strictly valid to use parametric statistics. However the parametric methods that we used are well known to be robust and for every parametric correlation coefficient given in this paper we also did a nonparametric test; these invariably gave similar results. We present parametric correlation coefficients where possible as these indicate what proportion of the observed variation is accounted for by the relationship. Nonparametric correlation coefficients are given where one or both of the two variates were ranked.

The Validity of the Aggressiveness Score

We compared each cock's response to an observer standing in front of its cage with its response to a stuffed stationary standing cock grouse with erect comb which it had never seen before. A hidden observer presented the stuffed cock for ten seconds on the end of a long pole. Fewer cocks showed threat and attack to the stuffed cock than to a human and more showed escape responses but the responses to both stimuli were highly correlated (Table II).

Was the aggressiveness score elicited by a human comparable with that elicited by a live cock grouse? After putting a live grouse crouching in a submissive posture in a movable cage in front of a cock's cage the observer recorded that cock's responses for four minutes from a hide. He next moved the stimulus grouse in front of the next cock's cage and so on for each of the 20 cocks. As cocks responded much less vigorously to the stimulus cock than to a human we had to record their response for four minutes instead of the ten seconds as above. The aggressiveness score elicited by a human observer was related to that elicited by live grouse outside the cage ($r = 0.79$ $P < 0.001$).

Could a cock's aggressiveness score be used to predict his response to a strange intruder cock presented inside his cage? We put the intruder inside each cock's cage only once for one minute to avoid any habituation by the home cock. Using the same intruder throughout we compared each home cock's response with his aggressiveness score. As the intruder sometimes crouched and sometimes stood he was not a standard stimulus. We overcame this by introducing him in a sequence random with respect to the home birds' aggressiveness scores. Although this could not prevent the possibility of extra variation in the home cocks' responses (i.e. extra because of the nonstandard stimulus) it did prevent bias in the results.

The brief aggressive response of each home cock to the intruder was ranked 1 — home cock attacked intruder 2 — called a ♀ or c but did not attack and 3 — did not call a ♀ or c or attack. These isolation cages were so small that the intruder was inevitably very close to the home cock and any movement by the home cock towards the intruder almost always culminated in the intruder being pecked.

Those cocks with the highest aggressiveness scores in the isolation cages (i.e. towards the observer outside the cages) were the ones most likely to call at and attack a strange cock put into their cage (Fig. 2).

These results confirmed that a cock's aggressiveness score towards an observer was correlated with his tendency to attack a conspecific.

The Consistency of the Aggressiveness Score

Although the mean aggressiveness score varied with season (Fig. 3) one may still ask: Is an individual cock's score similar in the same seasons in successive years? Also: does the relative aggressiveness of a number of individual cocks remain constant throughout the year?

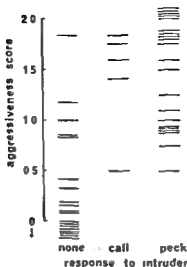


Fig. 2 The aggressiveness scores of cock red grouse in isolation cages compared with their responses to an intruder cock (April)

Eight cocks kept permanently in isolation cages had their aggressiveness scores measured 10 times in 1½ years. As the mean aggressiveness score varied with season we used correlations and not the statistic repeatability [Becker 1967]. All 45 possible correlation coefficients (r) between scores on different dates were positive with a median of 0.66 and a range of 0.21–0.99. A different result occurred with cocks which had not been permanently in isolation cages. In the interval between an aggressiveness test in autumn and a repeat in the following spring we had put these cocks into groups so as to rank their dominance (see below) in winter. When they went back to the isolation cages in spring their scores did not correlate with those of the previous autumn but by the next autumn they did (Table III). Thus experience prior to isolation may have affected the aggressiveness score but the score was repeatable when prior experience was held constant.

Do Cocks' Aggressiveness Scores Change When Their Environment Changes?

To study this we removed cocks from their isolation cages and put them into cages with three hens already present. Although these were larger (1.5 × 2.1 m) than the isolation cages the floor area per bird was the same. We made no attempt to determine the relative importance of change in cage size as against presence of hens.

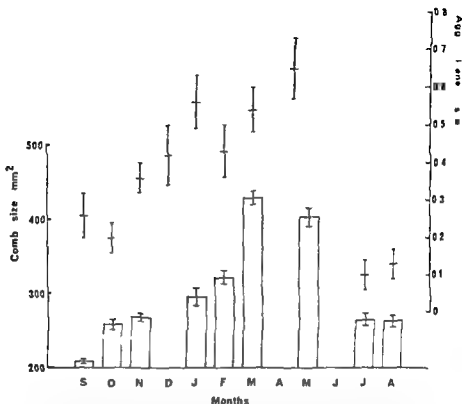


FIG. 3. Annual variation in comb size (bottom) and aggressiveness scores (top) of captive red grouse. As comb size increases with age, the data on combs here are for birds in their first 15 months of life only. The data are from several different groups of birds measured between 1969 and 1976. Means \pm 1 standard error.

TABLE III. Correlation Coefficients (r) Between Successive Aggressiveness Scores for Cock Red Grouse Which Were Moved Frequently During the Winter

Origin of eggs ^a	Dates of measurements	N	r	Significance level
1973 (W)	Oct 73 Nov 74	12	0.78	0.01
1974 (W)	Oct 74 Mar 75	34	0.04	NS
1974 (W)	Oct 74 Nov 75	11	0.63	0.05

^a(W) here and elsewhere indicates birds hatched from eggs taken from the wild

Each cock was left in his new cage for a few days and then his aggressiveness score was measured as above. The scores did not correlate strongly between one test situation and another but when the birds went back to the isolation cages their aggressiveness scores returned to what they had been previously (Table IV). Hence altering the environment changed aggressiveness scores but these changes were reversible.

Was the changed aggressiveness score of a cock in the large cage with hens present associated with a changed aggressive response to an intruder cock? As birds in these larger cages had a bigger area of floor and so more freedom of movement we could define more ranks for each cock's aggressive response than in the small isolation cages: 1 — home cock chased and pecked intruder; 2 — chased but did not peck; 3 — called a b or c and stepped towards intruder but did not chase him; 4 — called a b or c and 5 — did not call a b or c or move towards intruder. Cocks with high aggressiveness scores were more likely to chase and peck a strange cock (Fig. 4).

TABLE IV Correlations (r) Between Successive Sets of Aggressiveness Scores When Cock Red Grouse Were Moved From One Test Situation to Another and Then Back Again

Dates when scored	Experiment 1 (12 birds)	
	Situation	Correlations
Nov 9–25	hens present A ¹	A ¹ B = 0.127
Nov 27–Dec 7	cock isolated B	BA ² = 0.242
Dec 17–19	hens present A ²	A ¹ A = 0.769**
Experiment 2 (11 birds)		
Nov 10–19	cock isolated B ¹	B ¹ A = 0.329
Nov 29–Dec 11	hens present A	AB ² = 0.231
Dec 26–Jan 12	cock isolated B ²	B ¹ B = 0.667*

*Two-tailed $P < 0.05$ ** $P < 0.01$

Each of eleven cocks in isolation was successively scored for aggressiveness towards an observer presented with a strange cock inside the cage and ranked for his aggressive response to this intruder. Each was then moved into a large cage with three hens again scored for aggressiveness and finally presented with a second strange cock and ranked for his aggressive response towards him. The change in aggressiveness score towards an observer was correlated with the change in ranked aggressive response towards the intruding cocks ($r_s = 0.59$ $P < 0.05$).

DOMINANCE

Two methods for assessing dominance ranks are 1) pairing one individual against another in a neutral place and 2) observing agonistic interactions amongst members of a group. Both give similar results in red grouse [Kolb 1971]. We used group tests because they gave more data more quickly and also because many aggressive interactions amongst wild grouse in winter occur while the birds are in groups [Watson and Jenkins 1964].

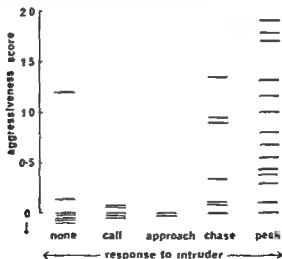


Fig. 4. The aggressiveness scores of cock red grouse in large cages with hens present compared with their responses to an intruder cock (Dec-Jan).

Description of Dominance Behaviour in Group Tests

When captive cocks were put together in a cage they threatened each other spontaneously and did so more frequently while competing at a food tray. They showed the entire range of threat and attack postures noted in wild cocks by Watson and Jenkins [1964]. Most encounters were settled quickly by threatening or attacking. Occasionally birds confronted each other in a horizontal "face to face" posture before one gave way but very rarely fought.

Measuring Dominance in Groups

Cocks that had been in isolation were put simultaneously into a cage in groups usually of eight. We identified each bird by a coloured leg ring and observed from a hide. Food was withdrawn for several hours during the day and then supplied in one dish immediately before our observations in the evening. When all eight birds in a group were together we could clearly distinguish the most dominant ones but birds low in the order seldom interacted and so provided very few data [Kolb 1971]. Therefore when a cock had been clearly the most dominant for two days we removed it whereupon another usually became dominant. By repeating this procedure we could rank individuals in the order in which we had removed them. We also recorded each individual interaction so as to calculate a dominance index [Butterfield and Crook 1968] for each cock. These dominance indices agreed well with the order in which we had removed the cocks. We used them to decide the dominance of a few birds which had failed to show clear despot/subordinate relationships.

When we had to rank more than nine birds at a time we separated them into groups of eight or less and ranked each group separately. Selected individuals from each group were then tested against individuals from other groups at least two weeks afterwards. This enabled us to rank each bird in a large batch against all others in it.

Consistency of Dominance Rankings

Dominance rankings were repeated at times varying from two months to two years. The statistic repeatability [Becker 1967] was not appropriate as the data were nonparametric. Repeated rankings were positively correlated in most cases significantly (Table V).

Dominance Ranks in Relation to Aggressiveness Scores

Having measured the aggressiveness scores of individual cocks in isolation cages we put them in groups immediately afterwards and ranked their domi-

TABLE V Spearman Rank Correlation Coefficients (r_s) Between Successive Dominance Rankings for Cock Red Grouse

Date and origin of eggs ^a	Dates of testing	N	r_s	Significance level
1968 (W) ^b	Oct 68 Mar 69	8	0.98	0.01
1968 (T) ^b	Oct 68 Jan 69	8	0.79	0.05
	Oct 68 Oct 69	8	0.60	NS
1968 (T) ^b	Nov 68 May 69	6	0.83	0.05
1969 (T) ^b	Oct 69 Dec 69	7	0.82	0.05
1969-1970 (W) ^b	Nov 70 Apr 71	7	0.64	NS
	Apr 71 Oct 71	7	0.72	0.05
	Nov 70 Oct 71	6	0.90	0.05
1970 (W) ^c	Feb 71 Sept 71	8	0.81	0.05
1971 (W) ^c	Oct 71 Nov 72	12	0.69	0.05
	Oct 71 Nov 73	11	0.75	0.01
1972 (W) ^c	Nov 72 Oct 73	12	0.83	0.01
1972 (T) ^c	Mar 73 Dec 73	8	0.56	NS
1973 (W) ^c	Mar 74 Oct 74	22	0.53	0.01

^a (W) birds hatched from eggs taken in from the wild (T) eggs from captive stock

^b Birds retested in identical groups

^c Retest of sample from a larger batch

TABLE VI Rank Correlations (r_s) Between Aggressiveness Scores and Dominance

Birds hatched	N	r_s
1971 (W)	11	0.79 *
1972 (W)	30	0.17
1973 (W)	14	0.31
1974 (W)	30	0.09
1974 (W)	41	0.07
1974 (T)	30	0.15
1975 (T)	34	0.17
1975 (T)	30	0.38 *
1975 (W)	47	0.28
mean r_s [Snedecor 1956]		0.19 *

* $P < 0.05$ $P < 0.01$

nance. The two measures showed only a small positive overall correlation (Table VI) but they did also when the aggressiveness scores were determined in the large cages with hens present ($r_s = 0.28$ $n = 36$ NS).

COURTSHIP BEHAVIOUR

Wild cocks with large territories tend to have more aggressive encounters and to win them more often than cocks with smaller territories and also tend to have more hens [Watson and Miller 1971]. We therefore anticipated that the aggressiveness and dominance rank of captive cocks should be related to their courtship behaviour.

Description of Test Situation

Courting cock red grouse show postures described by Watson and Jenkins [1964]. Our captive cocks courted infrequently but did so more readily in the following situation.

A cock which had been isolated for several weeks was put alone into a cage (1.2 X 2.4 m). After 24 hours a hen (the same in all tests) was introduced for an hour and the cock watched from a hide. By the end of the hour the cock had generally finished his display if any and sat quietly or walked about. To check that his responses were consistent we replaced the hen after 24 hours. Preliminary tests indicated that cocks responded to the second presentation within a few minutes or else did not respond at all. The procedure on the second presentation was therefore to note his reactions again for five minutes.

Ranking of Courtship Behaviour

Some cocks courted the hen in bouts lasting several minutes, others in a series of bouts lasting a few seconds each, and some only looked at the hen and partly erected their combs in brief flashes. Some showed no sexual interest. We ranked the cocks according to the total amount of time that they spent in courtship. Many cocks sang between bouts of courtship and the number of songs was noted.

In most cases a cock responded in the same way on both the occasions that the hen was put into its cage, but a few cocks reacted more vigorously the second time. This allowed us to rank some cocks which had earlier shown no sexual interest in the hen.

Ranking of Aggressiveness During Studies of Courtship

We also assessed aggressiveness during studies of the cocks' courtship behaviour towards a hen. This could not be done by measuring the parametric ag-

TABLE VII Rank Correlations (r_s) Amongst Behaviour Measurements of Single Cocks in Tests Where a Hen Was Put into the Cage

	Courtship	Song	Aggressiveness	
			To observer	To grouse cock
Dominance	0.93**	0.83*	0.82	0.63*
Courtship		0.89 *	0.76 *	0.90 *
No. of songs			0.81*	0.81
Aggressiveness to observer				0.66

Each r_s is a mean [Snedecor 1956] of 3 values ($n = 8 \ 8 \ 6$)

$P < 0.05$ $P < 0.01$ (two-tailed)

gressiveness score as the test was done over too short a period and in any case the aggressive behaviour of some individual cocks changed rapidly after we put in the hen. We therefore had to record each cock's aggressiveness by ranking. The ranks were: 1 – attacked observer during the test; 2 – threatened observer; 3 – called b or c; 4 – called a only; 5 – showed no aggressiveness to observer. When we had finished studying each cock's courtship we introduced a quiet and unaggressive strange cock (the same in each case) into the cage and then ranked the home cock's response to the stranger: 1 – chased and pecked stranger; 2 – chased it; 3 – walked towards stranger and called; 4 – called b or c; 5 – called a only; 6 – showed no aggressiveness.

The Relationship Between Dominance Rank, Aggressiveness and Courtship

Although the ranking of the cocks' dominance did not correlate very well with the ranking of their aggressiveness scores in isolation (DOMINANCE and Table VI) the cocks' aggressiveness and dominance were well correlated after the hen had been introduced for the measurements of courtship behaviour (Table VII). This was because the cocks' aggressiveness often increased markedly after the hen was introduced.

COMB SIZE BEHAVIOUR AND THE EFFECT OF TESTOSTERONE IMPLANTS

Measuring Comb Size

The red supraorbital combs of red grouse are a prominent feature in aggressive encounters and an important releaser for aggressive behaviour [Watson and Jen

TABLE VIII Correlation Coefficients (*r*) Between Change in Aggressiveness Score and Change in Comb Size of Cocks Moved from One Cage Situation to Another

Experiment 1 (12 cocks)			
From	To	<i>r</i>	Significance level
Hens present	isolation	0.77	0.005
Isolation	hens present	0.81	0.005
Experiment 2 (11 cocks)			
Isolation	hens present	0.54	0.05
Hens present	isolation	0.39	NS

kins 1964] Birds behaving aggressively raise their combs but submissive cocks lower them out of sight under their feathers. When erect, each comb is roughly semicircular in shape and has a frilled outer edge. After spreading the comb out, the observer measured length horizontally at the base and height from the base to the highest point to the nearest ½ mm. Length X height gave an index of comb size. As comb size increased with age, we have compared only cocks of the same year class.

Aggressiveness Score, Comb Size and Testosterone Implants

Aggressiveness score and comb size were greatest in spring and least in summer (Fig. 3). In eight out of the nine groups of birds tested, aggressiveness score was significantly correlated with comb size measured at the same time (median $r = 0.41$, mean $n = 29$). Within each group, individual cocks with high aggressiveness scores in the isolation cages usually had large combs and almost never small ones at the time when the scores were measured, whereas cocks with low aggressiveness scores had a variety of comb sizes. Among cocks tested with hens present, the aggressiveness score correlated well with comb size ($r = 0.70$, $n = 36$, $P < 0.001$).

Short term increases or decreases in aggressiveness score were accompanied by parallel changes in comb size. When cocks in isolation cages were moved to cages with three hens, changes in their aggressiveness score were correlated with changes in their comb size (Table VIII). We also measured comb size in 14 of the cocks used for studying courtship. In 10 of these, comb size had increased within 48 hours of the hen being introduced.

These results suggested that changes in androgen may have caused variations in comb size and associated behaviour. We tested this by implanting cocks with

TABLE IV Effect of Testosterone Implants (15 mg) on Comb Size and Aggressiveness Score of Cock Red Grouse (Means \pm SE) Implanted July 30

		July 27	July 30	Aug 3	Aug 5	Aug 9	Aug 11	Sept 14
Experiment (n = 5)	Comb size	277 \pm 9	278 \pm 7	340 \pm 9	372 \pm 12	435 \pm 8	440 \pm 8	484 \pm 9
	Aggressiveness score	0.4 \pm 0.2	0.3 \pm 0.1	0.5 \pm 0.2	0.7 \pm 0.3	0.6 \pm 0.2	1.0 \pm 0.3	1.4 \pm 0.4
Control (n = 7)	Comb size	312 \pm 18	312 \pm 17	303 \pm 20	318 \pm 10	306 \pm 12	300 \pm 16	320 \pm 20
	Aggressiveness score	0.1 \pm 0.1	0.1 \pm 0.1	0.2 \pm 0.2	0.2 \pm 0.2	0.1 \pm 0.1	0.1 \pm 0.1	0.3 \pm 0.2

15 mg pellets of testosterone under the loose skin at the back of the neck where upon comb sizes and aggressiveness scores increased (Table IV)

Dominance Rank and Comb Size

We measured the cocks' combs in isolation cages immediately before putting them into groups for ranking of their dominance. We again measured the combs of every cock that we removed from the group during the work on the ranking. Comb size was related to dominance (Table X). Also when we took the cocks out of the groups their comb size was usually more closely related to dominance than before they had gone into groups. Cocks starting with small combs but dominant in the group had grown larger combs when we removed them from the group. Subordinates starting with large combs had smaller combs when taken out.

TABLE X Rank Correlations (r_s) Between Dominance Rank and Comb Size (Length X Height in mm) of Cock Red Grouse Measured Before Being Put in Groups for Ranking and After Being Removed From the Groups

Test	No. of birds	Before	After	Improvement
1	8	0.60	0.77	0.77
2	8	0.42	0.61	0.61
3	8	0.43	0.61	0.37
4	7	-0.10	-0.16	0.54
5	7	0.43	0.58	0.42
6	7	0.68	0.71	0.63
7	6	0.77	0.75	0.09
8	7	0.14	-0.27	0.60
9	8	-0.50	-0.51	0.56
10	8	0.78	0.51	-0.53
11	8	0.40	0.71	0.64
12	7	0.82	0.86	0.55
13	8	0.50	0.67	0.65
14	7	0.47	0.43	0.17
mean [Snedecor 1956]		0.44***	0.52**	0.46***

The Improvement column shows the correlation (r_s) between the following two variables: 1) the difference between an individual's ranks for dominance and comb size before cocks were put into groups and 2) the change (ranked) in each individual's comb size while the cocks were in groups (see Fig. 5)

$P < 0.001$

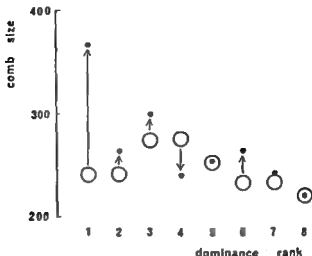


Fig. 5 Comb size just before (open circles) and just after (black spots) dominance ranking. This is test No. 1 in Table X.

shown by the 'Improvement' column in Table X with an example in Fig. 5)

Dominance and Testosterone Implants

The relation between comb size and dominance rank suggested that androgen may affect dominance. To test this we implanted cocks with pellets of testosterone. Having determined the dominance ranks of twelve cocks we selected six pairs where the two members in each pair were close to one another in dominance rank. The two were housed in adjacent isolation cages separated by a partition which we could remove when we wished to watch their reactions to one another. We first determined the dominance relationships of the six pairs and then repeated this 17 days later to ensure that the relationships were reasonably stable. Five of the six pairs showed the same dominance relationships towards one another the second time as the first. Only in pair three did the relationship remain remaining changeable throughout the experiment (Table XI). We then implanted each of four cocks that had been consistently subordinate with a pellet containing 15 mg of testosterone and when it had dissolved we implanted a second. The earlier dominance relationships subsequently reversed in four pairs. The frequency with which reversals occurred was significantly greater after the subordinate cocks had been implanted than it had been before implantation ($P = 0.024$ Fisher exact probability test).

TABLE XI The Effect of Testosterone Implants (15 mg) on Dominance Relationships in Pairs of Cock Red Grouse

Initial dominance order ^a	d 1 s	d 2 s	d 3 s	d 4 s	d 5 s	d 6 s
Date						
11/13/71	>	>	>	>	>	>
11/30/72	>	>	<	>	>	>
17/8/72				implanted		implanted
12/22/72	>	>	<	>	>	<
12/27/72	implanted				implanted	
1/24/73	>	>	>	<	<	<
2/2/73				implanted again		implanted again
7/14/73	>	>	>	<	<	<
3/1/73	implanted again				implanted again	
3/14/73	<	>	<	<	DEAD	<

^a The pairs are listed in order of the mean dominance rank of the two members. d > s means d dominant s s. Increased aggressiveness was shown about five days after implanting in all four implanted birds. Birds were "implanted again" when the first pellet had completely dissolved.

We already knew that implants of testosterone increased aggressiveness (Table IX) and thus again occurred in the present experiment.

Reversals in dominance occurred 2–11 weeks after implanting. The pair reversing at 11 weeks had had the highest mean dominance rank whereas the two pairs reversing at 2 weeks had had the lowest ranks (Table XI). The time elapsing before reversal was related to the aggressiveness of the unimplanted initially dominant cock. In short reversals occurred most quickly when the unimplanted bird was low in dominance ($r_s = 0.91$ NS) and in aggressiveness score ($r = 0.95$ $P < 0.05$).

DISCUSSION

Conclusions From This Study

A cock's dominance rank was more stable than his aggressiveness. Dominance was determined from social relationships amongst birds. Nonetheless it clearly had a physiological basis because both it and aggressiveness were correlated with comb size and increased after testosterone implants.

During the work on dominance ranking dominant birds with initially small combs tended to grow bigger ones whereas the combs of subordinates with initially big combs decreased (Table X Fig 5) These dominant birds with initially small combs which had shown little aggressiveness before being put in the group probably had to show more aggressiveness once in the group to achieve the dominance ranks observed To judge by comb size an increase in androgen accompanied this greater aggressiveness Conversely big-combed though subordinate birds in the group showed less aggressiveness than in isolation perhaps because they were being dominated This may have caused their combs and presumably their androgen activity to decrease Thus although androgen activity apparently affected aggressiveness and dominance the relationship also seemed to go the other way

Correlations between aggressiveness and dominance were almost always positive but varied in strength according to the situation in which the aggressiveness was measured (Tables VI and VII) That correlations were positive suggests that some factors determining aggressiveness also determined dominance for instance androgen activity That correlations were weaker in some situations than in others indicates that aggressiveness and dominance were partly determined by separate factors Correlations were weakest in the two situations (cocks in isolation and cocks with three hens) where the cock had been in that situation for some days and had no other cocks with which to compete This suggests that aggressive traits which could be freely expressed (or suppressed) in secure situations were inhibited (or brought out) in competitive or stressful situations Therefore the amount of aggressiveness that a cock shows is not necessarily the same as what it is potentially capable of showing

Aggressiveness increased a few days after implants of testosterone but the dominance relationship between a pair of cocks reversed in all four pairs up to 11 weeks after the subordinate had been implanted even though the two cocks had been close in dominance rank beforehand This suggests that reversals in dominance rank may have been due to the greatly increased aggressiveness of the initially subordinate cocks but that other factors were also important and delayed the reversals

This Study and the Literature

Dominance in chickens is related to circulatory androgens [Collias 1943 Allee Collias and Lutherman 1939 van Krey and Siegel 1968] and also to moult [Collias 1943] body weight [Craig 1968 Siegel and Siegel 1963] and inheritance [Ortman and Craig 1968] Therefore differences in the dominance of chickens reflect variability in the physiology of different individuals as in grouse

Whether learning is important in establishing and maintaining dominance relationships in grouse is unknown If however the stability in dominance that we

found had been partly due to memory there must still have been initial differences amongst individuals which were then remembered. As implants of testosterone increased a cock's dominance rank, memory cannot be the only factor. Furthermore, there is evidence that differences in the ability of cock grouse to dominate other cocks are inherited [Moss et al. 1974].

Syme [1974] pointed out that different dominance ranks, as determined by the competitive order in which individuals feed, drink, or avoid electric shock, do not always agree with each other. Although we limited food so as to stimulate aggression, our dominance rank is an aggressive rank in Syme's terminology as it was based solely on threat and attack, and not on which individual had prior access to food. Aggressive dominance ranks are generally stable and are useful predictors of other behaviour [Baenninger 1966, Guld 1958, Fidler 1977], and our results confirm both statements. Of particular interest is the observation of Poole and Morgan [1976] that the individual house mice (*Mus musculus*) most likely to get territories could be predicted from their dominance ranks as determined before they took these territories. Similarly, wild pheasant (*Phasianus colchicus*) cocks which were dominant at winter feeding sites also began to establish their territories earlier in the spring than did sub-dominants [Collias and Taber 1951].

Relevance of This Study to Research on Wild Birds

Although the behaviour of captive birds may include artefacts irrelevant in the wild, our results show several parallels with behaviour in the wild. 1) The aggressiveness accompanying call a is less than that accompanying b or c in the wild [Watson and Jenkins 1964] and in captivity (Table I). 2) In the wild [Watson and Miller 1971] and in captivity [Table VII, Marquiss 1977 and other unpublished data], the aggressiveness of different cocks is correlated with their frequency of singing. 3) In the wild, an index of aggression was related to territory size [Watson 1964] and cocks from a population at low density, and therefore with big territories, had bigger combs than cocks from a population at high density with small territories [Moss 1967]. In captivity, comb size was related to aggressiveness and dominance. 4) In the wild, cocks with large territories had more hens than cocks with small territories [Watson and Miller 1971]. In captivity, dominant cocks spent more time courting a hen than did subordinates. 5) After implants of testosterone, captive cocks became firstly more aggressive and then more dominant and aggressive. In the wild, an implanted cock encroaches on his neighbours' territories, initially losing most of the disputes that he has thus started, but subsequently winning many encounters [Watson 1970]. We conclude that behaviour in captivity shows enough parallels with the wild to indicate that it is a good basis for further experimentation.

Our finding that dominance and aggressiveness are sometimes only weakly related confirms that they are different kinds of behaviour [Kikkawa 1968] and may help explain some other observations on wild birds. In black grouse (*Tetrao tetrix*) a peck-order in a feeding flock off the lek was not related to aggressiveness (ie tendency to initiate disputes) on the lek [Johnstone 1969]. Watson and Miller [1971] who observed wild cock red grouse having encounters with neighbours at the boundaries of their territories noted that the result of such encounters was often that one bird gave way slightly. However they found no significant correlation between the mean result and frequency of such encounters in one of the two years of their study. Possibly their result of encounters is similar to our dominance and their frequency of encounters similar to our aggressiveness. Clearly aggressiveness and dominance are not the same in red grouse and it may be useful to distinguish them in studies of other wild animals.

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APPENDIX

Here we justify the method used for scoring aggressiveness by showing that a cock's aggressiveness score is linearly related to his tendency to threaten or attack an observer

First we devised a measure of aggressiveness which incorporated the minimum number of assumptions. This was Measure 1 the proportion of ten-second obser-

vations during which a bird attacked or threatened the observer. We ignored calls Attack and threat were combined to avoid assumptions about the quantity of aggressiveness indicated by each act. Although Measure 1 was therefore theoretically sound, in practice it had the severe drawback that only about half of the birds threatened or attacked in spring and in autumn only about one tenth of them.

Many cocks which did not threaten or attack the observer nonetheless gave the calls a, b, or c. Measure 2 for aggressiveness was based entirely on calls a, b, and c. The frequency with which a cock gave these calls was related to its aggressiveness in that cocks calling a, b, or c during a high proportion of the ten-second observation periods were more likely to threaten or attack the observer than cocks giving these calls during a low proportion of the observations (Table A I). Also, calls b and c were associated with more aggressiveness than call a: cocks which called b or c were more likely to threaten or attack than those calling a only (Table I). In a typical March sample, the relation between threat and attack on one hand and calling on the other was empirically described by the equation

$$y = 0.34x_1 + 0.73x_2 - 0.05 \quad (t_1 = 2.60 \quad P < 0.025 \quad t_2 = 7.99 \quad P < 0.001 \\ n = 69 \quad R = 0.72)$$

where y is Measure 1, x_1 the proportion of observation periods during which a cock gave call a only, and x_2 the proportion during which it gave calls b or c in addition to or instead of a. The left-hand side of this equation was a measure of aggressiveness and so, therefore, was the right-hand side. Dividing the right-hand side by 0.34 and adding 0.15 gave an expression

$$x_1 + 2.1x_2$$

which was linearly related to Measure 1 even though it was based entirely on calls. In Measure 2 for aggressiveness we allotted one point to a bird which gave call a only during a ten-second observation period and two points to a bird which gave b and/or c (with or without a). The aggressiveness score (Measure 2) was the number of points divided by the number of ten-second periods.

Measure 2 was adequate but had two drawbacks. Sometimes a cock called when the observer stood at the next cage but not in front of that cock's own cage a moment later. Table A II shows that a cock giving such "adjacent" calls was less likely to attack or threaten the observer than a cock which called when the observer stood directly in front of its own cage (i.e. frontal calls). A second drawback was that although direct observations of threat and attack were the most direct measure of aggressiveness, Measure 2 made no use of them.

Measure 3 was therefore devised and it is the one used in this paper and described in the text. Results from it were highly correlated with those from Measure 2 ($r = 0.92$, 69 cocks, 15 observation periods in March). Measurements by two observers who both used Measure 3 were also highly correlated ($r = 0.89$, 48 birds, 15 observation periods in January).

It would not have been a sufficient justification for Measure 3 to show merely that it gave results correlating with results from Measure 1 ($r = 0.87$, 69 cocks in March) as both methods had observations of threat and attack in common and thus were not fully independent. However, Measures 1 and 2 correlated well with each other even though based on quite different kinds of behaviour. Our main Measure 3 gave results very closely related to those from Measure 2 and therefore related to those from Measure 1 (ie the measure based entirely on direct measures of threat and attack). This crucial conclusion is not affected by the fact that Measures 2 and 3 had elements in common.

TABLE A 1 The Frequency With Which Cocks Called At and Threatened or Attacked an Observer Standing in Front of Each Cage

		Frequency of calls a, b & c	Percentage frequency of threat or attack			
			none	low	medium	high
Oct (142 birds)	none	53	0	0	0	0
	low	21	1	0	0	0
	medium	15	1	0	0	0
	high	6	1	1	1	2
April (63 birds)	none	25	0	0	0	0
	low	21	2	0	0	0
	medium	10	8	2	2	11
	high	5	6	8	8	14

Low frequency 1-33% medium 34-66% high 67-100% of observations
 * X² 3 contingency tables excluding birds which did not call and combining columns 2-4 were significant ($P < 0.001$) in both months. Each set of data is based on 18 ten-second observations made during nine days.

TABLE A II Number of Cocks Which Gave Frontal and Adjacent Calls* in Relation to Whether They Attacked or Threatened an Observer During 111 Ten Second Observations

		Attacked or threatened observer	
		yes	no
October			
Frontal	calls only	4	15
Adjacent	calls given	3	50
April			
Frontal	calls only	20	24
Adjacent	calls given	4	13

Frontal – cock called when observer in front of its cage *Adjacent* – cock called when observer in front of the next cage but not in front of cock's own cage

October: Fisher exact probability 0.116 April 0.114 combined $P < 0.1$

Book Reviews

Play and Aggression by Donald Symons New York Columbia University Press 1978 pp x + 246

This book opens with a report on field observations of social play among young rhesus monkeys who live freely on an island off the coast of Puerto Rico. The description encompasses the structure of social play patterns and an analysis of the age and sex of the participants. Far from being the *raison d'être* of the book, however, this description is but an hors d'oeuvre for seven chapters of discussion on the function of aggressive play among rhesus monkeys and certain other mammals.

The essence of Symons' thesis is that the adaptive function of behavior (in this case play fighting) may be gleaned from the structure of the behavior even in the absence of experimental proof. He argues convincingly that the play fighting of young rhesus monkeys is *designed* as practice for certain skills used by adults during fights. Although the monkeys seldom fight (about once a month on average), their position in the troop depends on performance during these rare fights. Ultimately aggression must pay off, or long ago the meek would have inherited the earth. The goal of play fighting is to deliver gentle bites to the partner while avoiding being bitten. The skills practiced during play fighting are how to maneuver oneself into a favorable position for biting, and how to counter one's partner's maneuvers. Symons asserts that to be given serious consideration, alternative hypotheses regarding the function of aggressive play must satisfactorily account for its design. I am sympathetic with his faith in the design of play behavior as an indicator of its function. Certainly the experimental school has not flourished in the field of play, whereas Symons' approach carries us a worthwhile distance on the strength of observation, intuition, and common sense.

Indeed, I felt that the strongest of Symons' arguments is that based on the declining human art of common sense. For example, he explains that it is nearly impossible to describe the most salient features of rhesus play fighting in traditional ethological terms because the fighting is a graded series of muscular movements endlessly variable in which each partner continually counters the other's moves with ever increasing skill. The ethologist may indeed be unable to detect the most significant movement strategies since he or she is probably not an expert

play fighter. Of course this comment might be made on other forms of professional criticism besides ethology.

During the discussion the reader is taken on a guided tour of prevailing ethological notions on mammalian play. With chilling (and overdue) use of the common sense weapon Symons pares away many of the current clichés concerning play. One such concept which seems to underlie much misunderstanding of playful behavior is the structural comparison that ethologists as opposed to young animals make between play fighting and fighting.

In the popular academic view actions such as biting during play are accompanied by specialized metacommunicative signals which constantly remind the partners that the actions are not serious. In the simian view as interpreted by Symons however play biting and biting are altogether physically different modes of mouthing contact. Monkeys can communicate about what they are doing with communicating about what they are not doing. The ethologist may not use the same cues as the young monkey to distinguish play fighting from fighting. The distinction may not even be important to the young monkey who hardly ever fights in any case.

More serious pollution of the literature on animal play is caused by the idea that a prominent function of play is to generate novel behavior patterns. Symons conducts a richly deserved and dignified funeral service for this idea. The basis for the novelty theory was the seeming variability in the combination of different motor patterns during play when compared with serious behavior. From such juvenile experimenting novel behavior could even must arise. From his observations however Symons believes that play fighting results in all monkeys learning the same or very similar tactics. In other words play trains monkeys to be highly skilled conservatives.

I have one major criticism. The subject is largely the function of play fighting by a single species and in this limited context it makes at least to me excellent sense. From the start of the discussion however Symons falls from grace by using the bald expression 'play' as either an intentional or unintentional substitute for 'play fighting by young rhesus monkeys'. Thus discreet sliding from the particular to the general is quite unjustified since almost all the illustrations he uses are from rhesus monkeys and a few other primates and an occasional carnivore. By making this generalization Symons manages to create or to perpetuate a controversy which need not exist. He says (p. 101) 'That by playing animals practice and perfect specific skills would seem to be so obvious as to be nearly beyond dispute to many observers of animal play' yet it is not widely accepted and many students of play maintain that there is good evidence against it. Symons has momentarily forgotten that there are many kinds of mammals besides Primates and Carnivora these different mammals may and do sometimes play in a manner quite different from that of rhesus monkeys and their play may have a different function.

Much of the discussion in this book could have been written without Symons' own observations with which the book opens. Literature already published would largely have sufficed. The author, however, evidently developed his uniquely intuitive grasp of play fighting from his personal experience of watching. Therefore I feel the detailed presentation of his results in the book is justified.

To the dwindling minority who still pick up an ethological volume in anticipation of pleasure, I recommend this book. Not only are the photographs evocative of the play mood and the prose delightful, but the social role of football in England is discussed most intelligently in the later pages, and there is also a photograph of a rhesus monkey sitting in a tree reading.

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Analysis of Delinquency and Aggression edited by Emilio Ribes Inesta and Albert Bandura. Hillsdale, New Jersey: Lawrence Erlbaum, 1976. pp. v + 273.

This book contains the papers given at the Third Symposium on Behavior Modification held in January 1973 under the auspices of the Department of Experimental Psychology and Methodology of the National Autonomous University of Mexico. The symposium was planned around two themes, namely, the experimental analysis of aggression and the application of learning principles to preventing and modifying delinquency.

The ten papers each stand as individual contributions. They provide discussion on sociological issues in the control of human aggression and delinquent behavior (by E. Ribes Inesta), discussion of some of the problems raised by experimental research on aggression by animals in laboratory settings (by J. D. Keehn) and on the technology for measuring and modifying transgressive behavior (by R. Schitzgebel); they give descriptions of the use of certain corrective techniques for delinquents in institutional environments (by B. Domingues et al. and by I. Sarason) and of preventive measures introduced into the environments of aggressive and delinquent young people (by J. D. Burchard et al., by J. B. Reid and G. R. Patterson, by H. L. Cohen, and by E. L. Phillips et al.) and finally they include a presentation of social learning theory (by A. Bandura).

The theoretical position taken throughout the book is that human aggression and delinquency are social responses which can be fully controlled given an appropriate social environment. Evidence for this belief is put forward in several papers, principally in the contributions by the editors. They contrast it with other

theoretical viewpoints which present aggression as a drive as an urge released by organismic or environmental events or as a response to frustration. Bandura considers that the explanatory power of theories such as these is small whereas social learning theory can provide a general system sufficient to cover all facets of aggression.

There is no doubt that social learning theory has been helpful in planning strategies by which violence and delinquency may be reduced. The projects which describe social interventions designed to reduce aggressive behavior all report promising results. It is however noteworthy that each project presented at the symposium is for one reason or another on a small scale that some recalcitrant subjects were met and that there is no discussion of possible factors that might distinguish responsive subjects from nonresponsive.

One is left with the impression that the contributors tend to be overoptimistic about the extent to which violence and delinquency can soon be eliminated by social engineering. For instance Ruben Inesta advocates the control if not the elimination of human aggression through far reaching social changes in which a) social wealth is equally distributed b) aversive controls are eliminated and c) violence is no longer legitimized as a means of appropriating socially produced wealth. He does not however discuss possible strategies through which social scientists would deal with the aggressive reactions that tend to arise whenever established life styles are threatened by change.

Nevertheless as Schitzgebel says effective practice does not necessarily require valid explanatory statements. These papers have much to recommend them. The book will be found helpful by all who are dealing with problems of human aggression and who are interested in finding alternatives to punishment in handling delinquent children and adolescents. It is well produced and easy to refer to.

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Children In Conflict Growing Up in Northern Ireland by Morris Fraser New York Basic Books 1977 pp ix + 167

There have always been two populations in Ireland. The original inhabitants have been supplemented by waves of Protestant settlers from England and Scotland who came on their own account or were planted in the sixteenth and seventeenth centuries by the English government. There has always been trouble

between them. The present eruption dates from 1969 and differs from the others only in that up to date technology has been added to skill in fighting with improvised weapons. The current situation in Ulster has been ascribed by Thomson [1976] in his history of an Anglo-Irish Family planted three centuries ago in Sligo to segregation, the inability of natives and settlers to live together in one society, the settlers' fear and their determination to hold exclusive power. These he believes are the causes of violence now as they were in 1798.

This is also the thesis advanced by Dr Fraser in his book *Children in Conflict*. His experiences as a child psychiatrist in Belfast have led him to the view that the Ulster conflict is not a holy war between equals but a situation which arises anywhere in the world where ethnic minorities are discriminated against by insecure majorities. The flash point comes inevitably when both the size and economic situation of the minority begins to approach that of the majority. At that point any protests by the minority against the discriminating tactics of the majority are met by aggressive reactions on the part of the majority and the fight is on.

Dr Fraser's evidence comes from a study of figures for psychiatric admissions, outpatient attendance and drug prescription rates, from the analysis of interviews with some 250 children, from observation of the behavior of the public and the media and from a review of the literature on the effects of wars and riots on children.

Dr Fraser's theoretical stance is eclectic. He considers it beyond the scope of the book to review the many theories about aggression which he feels break down when an attempt is made to fit a single theory to all situations. In order to understand the violent gang behavior of children in the Ulster setting, he suggests a three stage sequence that he considers applicable in most areas where ghetto youth finds itself in conflict with authority. There has to be a presence such as a British soldier, that the child defines as a bogeyman, fear has to be aroused to a point where the child is obsessed with fantasies of getting rid of the bogeyman and then, given specific conditions and cues, these fantasies are translated into action.

The findings show that ill effects, particularly on children, come from living in a state of constant expectation of personal damage and of loss of family, home and friends — especially when family, friends and the media, by their behavior and remarks, contribute to the state of apprehension.

Two profiles of children especially at risk have been identified. One is exemplified by children, often girls, about 10 years old. They have always been prone to physical illness and overanxiety, they are economically deprived, one parent is absent or chronically ill and one adult in the immediate family has crippling symptoms of anxiety and is given to ruminating aloud on past and future catastrophes.

The second profile describes the young terrorist. It is exemplified by boys in their early teens who are economically deprived, with one parent involved in the

Republican movement or interned. These boys are mentally preoccupied by thoughts of conflict, have no other interests, are leaders of gangs, and direct hostility towards all authority including parents.

Children in Conflict is a well written book, and useful despite the absence of an index. It is to be recommended to politicians as well as psychologists, sociologists, and psychiatrists. Dr Fraser's views and findings deserve further study. Should they be confirmed, not only will our understanding of the roots of civil violence be improved but also our power to reduce it.

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Civil Commitment and Social Control by Martin L. Forst. Lexington, Massachusetts: Heath, 1978. pp vii + 175.

The Civil Commitment Statutes in Anglo Saxon legal systems are currently under review by scholars and legal philosophers who try to assess their effectiveness in dealing with specific classes of deviants. Originally these laws had benevolent and humanitarian goals. But, as various scholars in the field have pointed out, lack of procedural safeguards has led to abuses and mismanagement.

The book by Forst reviews the application of one such enactment, California's "mentally disordered sex offender" (MDSO) statute. The research has been conducted in three counties (Contra Costa, San Francisco, and Orange) by analysis of official records, interviews of key decision-makers, and the use of a questionnaire given also to decision makers, including an evaluation of the gradient of offence severity. The history and the use of MDSO statutes are also reviewed. The application of MDSO provisions does not vary greatly in the three counties, although some disparities are noted.

It appears that the MDSO civil commitment has now been criminalized to a degree that makes it indistinguishable from criminal sanctions. After the "trial" of the case is assessed, and after plea bargaining, a sanction matching the "going rate" in the state is selected. Consideration of the needs of the individual, which should be the main (or only) factor for the use of the MDSO, are minimal. MDSO commitments range in severity from imprisonment in the county jail to a sentence to a

prison. Normally the offender stays at Atascadero (the institution for MDSO offenders) for about two years. Opinions on the effectiveness of therapy available at Atascadero are not optimistic. When the Atascadero staff began recommending offenders for earlier discharge, the Supreme Court began to impose additional criminal penalties to avoid a reduction in time served. Essentially, the time in detention, either criminal or civil, seems to be the crucial factor in policy on sentencing.

In practice, therefore, there are not two separate sanctioning systems, but only one. The defense attorneys seem to be fully aware of the situation and to use it to secure release of their clients by intervening at the (estimated) appropriate time regardless of the merits of the particular case.

The author formulates sensible policy recommendations. Both for humanitarian and for practical reasons, he does not advocate repealing the MDSO statute. He believes, however, that MDSO commitment should be voluntary. It should be raised as a sentencing alternative only by the defense just as with criminal insanity. An alternative recommendation is that provision should be made to ensure that the duration of the civil commitment should not exceed the statutory maximum of a criminal commitment. Since most of the cases are felonies, this would not alter current practices, but the risk of excessive sentences for misdemeanors would be avoided. The Atascadero staff should also periodically assess the patient's progress and inform the court.

Greater procedural protection is given to mental patients and to offenders under civil commitment, and this trend is likely to continue. This is in keeping with similar trends in the juvenile justice system, as is evident in the *Gault* case. Another trend is to require strict standards of proof (as in criminal cases) for decisions on civil commitment.

Various recent cases involving these and related issues are discussed in detail in the concluding chapter. The author considers, correctly in my opinion, these trends to be favorable. Criminalization of the "civil" commitment procedures would increase procedural and substantive protection in civil commitment law, decrease disparities and reduce inconsistencies due to the use of discretion. In spite of the small sample reported, the book is recommended as one of the few existing empirical studies of an important problem. Such research should be repeated elsewhere.

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Genotype and Environment in the Social Interactions of Wild and Domestic "Norway" Rats

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Wild rats *Rattus norvegicus* (a) trapped as adults or (b) of the second generation in captivity (lab wild) and domestic rats of two strains were studied for 28 days in artificial colonies in large cages with attached nest boxes. Controls were kept in mated pairs in small cages. Each colony consisted of six males and six females. The interactions of the males in six colonies of trapped rats were highly "stressful" 61% died and most of the survivors lost weight and had greatly enlarged adrenals. In each colony however there was a male (an alpha) that gained in weight and spent much time during the dark hours in the open on the floor of the cage and in three colonies there were also other males ("betas") that gained in weight. The adrenals of alphas and betas weighed about the same as those of the controls. In one of the 12 colonies of domestic rats one male behaved like a wild male but in the other colonies the males gained in body weight and their adrenal weights resembled those of the controls. In three colonies of lab wild rats 227 of the males died but there was no evidence of males of different status. The findings confirm that the "agonistic" behavior of domestic rats is usually much attenuated in comparison with that of the wild type. A number of methodologic implications are discussed.

Key words: aggression wild rats domestication territory agonistic behavior adrenals

INTRODUCTION

Rattus norvegicus the common brown or Norway rat occurs in most regions of the world as a commensal with man and hence as a serious pest. It is also universal in centers of learning as the laboratory rat. The attribution of laboratory rats to this species is based on breeding. The many strains of laboratory

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rats can interbreed and domestic rats can be crossed with wild *R. norvegicus*. Features of the behavior of such hybrids have been described by Stone et al [1932], Barnett [1960] and Boreman et al [1972]. They tend to be intermediate between the parental types.

There are however differences of opinion on the social conduct of the domestic varieties especially their aggressive behavior and on the category to which such behavior belongs. Barnett [1975] has stated that domestic rats differ from the wild type in that some components of threat (including attack) have been lost or greatly attenuated and the fighting that remains is usually unma and does not produce ill effects. But some workers have described what they call aggressive or agonistic acts among laboratory rats (for example Flannelly et al [1977], Grant [1963], Taylor [1976]). These acts include allogrooming, crawling over or under another rat, adopting an arched back posture with flank presentation and mounting from the rear. Taylor [1976] however remarks of his observations that attacks with biting were infrequent. Blanchard et al [1977] have described exceptionally fierce clashes among laboratory rats but these occurred only after many weeks of special treatment.

Two types of evidence are relevant to these apparently opposed positions. 1) One is detailed quantitative description of actual movements in encounters which can show whether there is a decisive behavioral difference between the two kinds of rat. The comparison should be between adult males that have been living in groups. Isolation has complex effects that make interpretation of the resulting behavior difficult (reviewed by Barnett [1975]). In a typical attack by a wild male the initial approach is slow and is accompanied by urination and defecation, the hair is raised, when close the attacker usually presents its flank to the other and briefly prances around on extended legs with the back arched (the threat posture). The attacker then makes a sudden leap with repeated adductions of the forelimbs and a momentary bite [Barnett 1958a]. Among domestic rats as far as we know this full sequence has not been observed. Such rats may perform some components, for instance the threat posture, and other features of encounters between males such as boxing (in which the two animals stand upright facing each other) also occur. Allen [1977] has staged encounters between pairs of wild rats and observed a high incidence of attack. In encounters between laboratory rats in identical conditions attack hardly occurred.

2) Secondly encounters between wild males can produce in the animal attacked a failure to eat, a decline in body weight, hyperactivity and enlargement of the adrenal cortex, collapse and death even in the total absence of wounding (reviewed by Barnett [1975]). Such changes can be recorded without ambiguity. In the account that follows we give information on body weight, mortality and adrenal weights but no detailed description of the accompanying social interactions. Our procedure allows exact statements on differences between the wild type and domestic forms in specified conditions. Hence it

becomes possible to decide to what extent domestic rats display some of the characteristic changes of social stress [Barnett 1964]

Most of the problems of social stress in mammalian populations remain unsolved but in recent years they have been shown to have a wide scope. Evidence comes from the work of von Holst [1969, 1972b] on the tree shrew *Tupaia belangeri*. The effects of intolerant behavior among male tree shrews closely resemble those observed in wild rats. In addition, the kidneys of attacked tree shrews develop pathologic changes [von Holst, 1972a]. Similar renal pathology has been observed among male long haired rats *Rattus villosissimus* after exposure to attack [Barnett et al. 1975] and in exceptionally dense natural populations of the same species (J. L. Carstairs unpublished findings).

Our objectives therefore were mainly methodologic: 1) To distinguish some of the effects of social interactions displayed by the two types of rat; 2) to examine whether the problems of rodent social behavior can be effectively studied in experiments on the convenient domestic forms; and 3) to put the behavior studied in its appropriate category.

METHODS

The Rats

The wild rats were all of the species *R. norvegicus* trapped in Sydney. Those used for the first three colonies and their controls were taken as adults from a large population on a university campus. Those of the other three colonies were trapped as young adults in a thriving colony associated with dog kennels.

On arrival in the laboratory they were sprayed with a solution of 2 ml Maldison in a liter of water to remove ectoparasites. They were then kept for at least two weeks in wire cages described by Barnett and Prakash [1975] designed for wild rats in groups of three of like sex. For two weeks they received 0.1 gm Mebendazole powder (methyl 5-benzoyl-2-benzimidazole carbamate) in 100 gm food to remove endoparasites. If there were signs of bacterial infection the rats received 0.5 gm tylosin tartrate in each liter of drinking water.

In addition, some wild rats of the second generation bred in captivity were studied separately. They had been bred and kept in similar small cages according to the procedure described by Barnett [1958b]. In this paper they are called lab wild rats.

The domestic rats were of two strains both supplied by the John Curtin School of Medical Research. One was agouti (wild type in color) the other was hooded. They were kept in conditions similar to those for the wild rats but in groups of six or seven. Their ages were from 24 to 32 weeks at the beginning of the experiment.

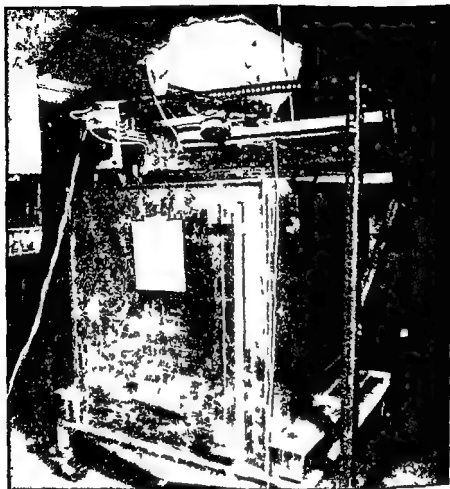


Fig. 1. Colony cage equipped for time-lapse photography. Two nest boxes are seen at bottom right. The vertical column on the wall of the cage is a food hopper.

Equipment

Colonies were set up in cages of which the floors measured 100 x 80 cm. The walls were 200 cm high. At floor level there were entries to four nest boxes which provided darkened refuges for the rats. Cotton wool was provided for bedding. The top of each cage was open.

Over it was suspended a camera set to take single flash light photographs of the cage floor at intervals of 30 min (Figs 1-2). The room with the cages was windowless. Artificial light was on from 6.00 AM to 6.00 PM. The camera was

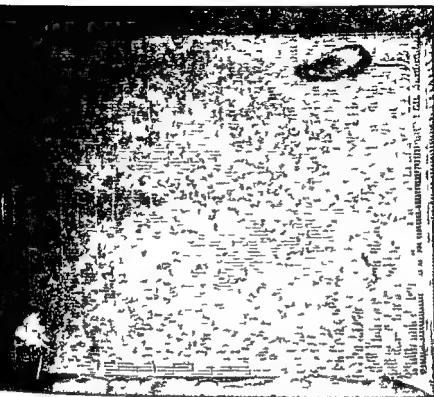


Fig. 2. Colony cage from above. A single wild male occupies the arena. Bedding has been dragged out of nest box near the waterspout at bottom left.

switched on from 4:00 PM to 8:00 AM on day 1 and on every third day thereafter throughout each experiment. Apart from occasional failures, the photographic record therefore covered the whole of the dark period and two hours before and after it on each of nine days.

Procedure

Twenty-one colonies were set up, three at a time. The rats of each colony were all put in the cage together at about 4:00 PM. There were six colonies of trapped rats and three of second-generation laboratory bred wild rats. For convenience in distinguishing the sexes, six colonies of domestic rats were of hooded males and agouti females, and six were of agouti males and hooded females. Corresponding to each batch of colonies (except those of the lab wild rats) there was a group of controls. These were mated pairs in standard small cages, each with one nest box of the same kind as those used for the colony cages. Controls for the wild rats

were matched as closely as possible for body weight and origin. Those for the laboratory rats were litter mates of the animals in the colonies. A standard rat diet and water were available at all times.

Each colony consisted of six males and six females, all adults and all apparently healthy. The males of each colony were from the same habitat, but different holding cages. All males were weighed to the nearest 1 gm, marked with Durafur and put in the cage within a few minutes of each other. They then remained in the cage for 28 days. If a rat died, the body was removed; if it had very recently died, it was weighed and a postmortem examination was made, as described below. At the end of the experiment all surviving rats were removed, killed and weighed. Wounds were recorded. The adrenals were removed and weighed to the nearest 0.1 mg on a direct reading balance. The lungs were examined for signs of infection.

As a result of this procedure, some of the figures of body and adrenal weights were of wild males that had been exposed to the experimental conditions for less than 28 days. The observed differences from the controls would probably have been greater had all experimental rats survived for the full period.

Statistical Analysis

Comparisons between colonies and controls, and between different classes of animals in the colonies, were by Student's *t* test (two-tailed). Within class homogeneity of colonies and control groups was tested by one-way analysis of variance. This test showed the colonies of laboratory rats not to be homogeneous. Hence in the statistical analysis the mean of each colony was treated as a single replicate.

Covariance analysis was carried out to test for the validity of comparisons of the relative adrenal weights of different classes.

RESULTS

Social Structure of Colonies

Trapped rats. Figure 3A illustrates some of the social interactions of wild rats revealed by the photographic record. During the dark period, even on day 1, it was unusual for more than one male to be out of the nest boxes at a time. Often one appeared in a series of frames; it was therefore probably in the open on the floor of the cage continuously for many hours. Such a male we call an alpha male, but do not, however, imply by this the existence of a typical status system (dominance hierarchy) in these colonies. Direct observation showed that alphas attacked other males in the manner described in previous studies (see Barnett [1975]).

Although a male was out for most of the night on nearly all days in three of the six colonies, it was not always the same male. In those colonies we call only the male that was out during the later part of the experiment an alpha.

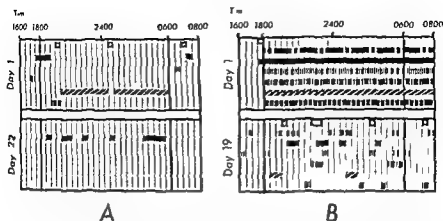


Fig. 3. Examples of records provided by time lapse photography. Photographs of the floor of each far e cage containing a colony were taken at intervals of 30 minutes throughout the dark period and for two hours before and after dark. The six males of a colony are each represented by a horizontal bar of a distinctive pattern. A bar indicates the presence of a rat in the frame exposed at the time indicated. A. Record of a colony of wild rats on days 1 and 22. On day 1 only one male was out frequently. This male was later displaced by another, and the latter was the only male to appear in the record on day 22. B. Record of a colony of domestic rats on days 1 and 19. On day 1 all males were out on the floor of the cage at all times after dark fall. On day 19 all males were out frequently during the dark period.

Females (which were not individually identified) behaved quite differently. At least one could be seen in almost any frame, and often two or three. There was therefore no evidence of any social restriction on their movements.

Laboratory bred wild rats. The behavior of the lab wild males was different. On day 1 all males were frequently out on the cage floor, even during the dark period. On later days, however, the pattern resembled that of the wild colonies. In one colony a single alpha had emerged by day 4; in a second colony all males were still frequently out on day 4, but there was an alpha from day 7. In the third there were two alphas from day 4 to the end.

The lab wild females behaved in the same way as the wild females.

Laboratory rats. The laboratory rats of both types (Fig. 3B) behaved like the wild females. On day 1 the exploratory tendency had full scope. At any time during the dark period several males and females were always out. Sometimes groups of both sexes slept in the open on accumulations of cotton wool. There was no evidence (except in one colony) of differences in status.

In the exceptional colony (RwL) the males were of the α_{out} type. One male was an alpha throughout. The females, as in the colonies of wild rats, were affected.

TABLE I Mortality in the Colonies

	No rats of each sex	Mortality		Mean days to death (range)	
		M	F	M	F
Trapped	36	22	10	14.5 (1-28)	17.9 (13-23)
Lab-wild	18	4	1	22.25 (17-27)	16
Domestic	72	4	0	13.25 (10-20)	-

Mortality and Body Weights

Trapped rats Table I gives the numbers of deaths in the colonies. There were no deaths among the controls kept as mated pairs. The main feature was the high death rate (61%) among the wild males. The trend over time for each colony was toward a group of thriving females and only one male, and in fact in three colonies only one male survived the alpha. This confirms previous findings on rats of the same species trapped in Scotland [Barnett 1958a]. There was, however, a high death rate (28%) among the females than that observed before. Many surviving males and some surviving females had superficial injuries, usually of the tail. There was no evidence of respiratory disease in any of these rats.

Mean changes in body weight are given in Table II. For this analysis the survivors from the colonies are divided into two groups: those that gained in weight and those that lost (omegas). All alphas gained in weight. In addition in colony A a second male, and in colony F three other males, did so. In terms of change in body weight and of organ weights, the alphas and the four others (which we call betas) form a single class, distinct from the omegas. All the controls gained in weight.

Table II also gives initial and final weights. The mean initial weight of the alphas plus betas was much above that of the omegas. Evidently survival was positively correlated with superior weight.

Laboratory-bred wild rats Four of the 18 males in the lab wild colony died (Table I). There was no evidence of respiratory disease in any of them. All the females survived. All males lost weight. Hence body weights gave no grounds for separating these males into two classes.

Laboratory rats Of the 12 colonies of laboratory rats, there were deaths in only three (Table I). One male died in colony II, and two in colony C. On examination of the lungs all these were found to have extensive chronic respiratory disease. One male died in colony II for no known cause.

In all colonies of domestic rats, except one, the males (apart from those that died) gained slightly in weight (Table II). Among the agouti rats there was no

TABLE II Body Weights of Males (Means \pm SE)

	Colonies				Controls			
	N	Initial wt gm	Final wt gm	% Change	N	Initial wt gm	Final wt gm	% Change
Trapped								
a	10	419.2 \pm 30.0	454.5 \pm 29.8	+7.9 \pm 1.5				
w	13	324.9 \pm 25.8	267.7 \pm 23.3	-17.0 \pm 3.7	18	360.9 \pm 18.2	381.1 \pm 20.2	+4.9 \pm 1.1
Lab wild	14	392.0 \pm 70.7	338.9 \pm 18.3	-12.9 \pm 7.0				
Hooded ^b	6	253.2 \pm 7.1	257.2 \pm 8.4	+1.3 \pm 1.3	24	253.6 \pm 3.9	270.3 \pm 4.7	+6.0 \pm 0.9
Agouti ^b	5	747.7 \pm 1.9	254.2 \pm 1.9	+2.6 \pm 0.8	24	245.2 \pm 6.1	254.0 \pm 5.6	+3.7 \pm 1.5
Colony R w L	6	255.5 \pm 7.0	727.7 \pm 12.0	-10.2 \pm 2.3				

^aComparison of percentage changes of colonies with those of controls^bEach colony of these classes was treated as a single replicate

dence of any difference in this regard between the colony members and the controls. But the hooded laboratory rats in the colonies gained less weight than the corresponding controls.

In the exceptional colony (RwL) the males were of the agouti strain. Although there were no deaths, this colony resembled a colony of wild rats in important respects. Only one male gained in weight. This male was initially the second heaviest of the colony (268 gm); the heaviest was 286 gm. At the end of the experiment it had gained 6% in body weight, and it was the only male in good external condition without bites. Hence in the analysis that follows colony RwL is treated separately from the others.

Adrenal Weights

Mean adrenal weights are given in Table III. Those of the alphas and betas did not differ from the control value, but the adrenals of the omegas had evidently undergone a marked hypertrophy. The differences from both the alphas and betas and the controls, however calculated, were statistically highly significant. The adrenal weights of the lab wild rats were intermediate between those of the

TABLE III Adrenal Weights of Males

	Colonies		Controls		P <
	N	Mean \pm SE	N	Mean \pm SE	
Absolute weights mg					
Trapped					
$\alpha + \beta$	10	101.3 \pm 11.1			0.2
ω	13	123.1 \pm 6.9	18	86.3 \pm 3.5	0.001
Lab wild	14	110.3 \pm 6.9			0.01
Hooded	6 ^a	49.4 \pm 2.0	24	51.8 \pm 2.6	0.7
Agouti	5 ^a	39.6 \pm 1.1			0.7
Colony RwL	6	46.1 \pm 4.1	24	37.9 \pm 1.5	0.05
Relative weights mg/100 gm					
Trapped					
$\alpha + \beta$	10	120 \pm 1.2			0.6
ω	13	48.8 \pm 4.7	18	24.0 \pm 1.3	0.001
Lab wild	14	33.4 \pm 2.4			0.01
Hooded	6 ^a	19.5 \pm 0.9	24	19.4 \pm 1.1	1.0
Agouti	5 ^a	15.8 \pm 0.5			0.5
Colony RwL	6	20.3 \pm 2.1	24	14.9 \pm 0.5	0.001

^aEach colony of these classes is treated as a single replicate.

wild alphas and betas and those of the omegas. Among the laboratory rats, once again, the only effect of the experimental treatment was on the adrenals of colony RWL.

DISCUSSION

Experimental Design

The defects of the work described above arise from its inadequate scale imposed partly by the difficulties of getting wild *R. norvegicus* in Australia. In our experiments there were two sources of variation: 1) Genotypic (wild contrasted with domestic) and 2) environmental (reared in freedom or in captivity). In its simplest form, this gives a 2×2 design. Unfortunately, one cell was missing — domestic rats reared in freedom. Moreover, for a comprehensive account of the effects of both variables, the number of cells would need to be increased in both dimensions for the following reasons:

1) There are not two genotypes, but many. Wild rats are genetically diverse. We know little of how the diversity influences behavior, but selection in the laboratory, intentional or inadvertent, has frequently revealed it (reviewed by Barnett [1975]). Laboratory rats too vary genetically in many ways between strains [Robinson, 1965]. The two types of successful rat in the wild colonies may reflect genetic differences. Barnett [1958a] described wild males called betas which survived and grew well in artificial colonies despite the presence of an alpha that tended to attack all other males. The betas did not attack intruders and they withdrew on the approach of an alpha. Nothing is known of what enables such rats to survive when other males do not.

2) There is an important environmental effect easily overlooked — the nurture provided in utero and in the nest by the mother and sibs. Our lab wild rats were of the second generation reared in captivity. They were therefore products of selection in captivity, rearing in captivity, and the maternal environment provided by females of the first generation reared in the laboratory. These females in turn represent a population differing from the original wild population: a) They had been reared in captivity; b) they were the result of selection at two stages — first trapping is not a random process, but selective, and second, only some females are fertile in captivity.

The Category of Behavior Studied

Another question of method concerns the kind of behavior we studied. It is commonly referred to as aggressive, but this term is now used so indiscriminately that it covers nearly all social interactions, as well as some which are not social, such as predation.

The conditions in which the colonies were kept allow wild rats to thrive, unless there are special sources of conflict [Barnett, 1958a], hence death and other ill

effects (including adrenal hypertrophy) cannot be attributed to the nonsocial features of the environment. Our findings therefore concern measurable effects of social interactions. Previous work cited in the introduction had also shown how in dyadic encounters threat by a conspecific can lead to loss of weight, adrenal enlargement, and death. By threat we mean a signal or display that tends to cause the withdrawal of a conspecific. *This definition includes actual attack and biting (or other wounding)* for these can presumably induce withdrawal. Threat in this sense is usually performed by adult male wild *R. norvegicus* in a familiar place; it is directed toward newcomers (which must also be adult and male). It is therefore territorial [Barnett 1958a]. To call it territorial behavior is not to explain it as Moyer [1976] supposes, but to classify it. It is territorial by definition.

The Effects of Domestication

Our findings allow some conclusions (summarized in Table IV) both on the differences between wild and domestic *R. norvegicus* and also on the effects of breeding wild rats of this species in captivity. For comparison with the wild type, the two strains of laboratory rats, though different in detail, may be treated together (colony Rwl excepted).

The contrast in behavior between the domestic and wild types is confirmed. In each colony of wild rats a single male behaved on the floor of the cage as if on his territory. During most of the dark period, other males were usually confined to the nest boxes. Farr et al. [1977] describe a similar effect of status relationships on the circadian rhythms of deer mice, *Peromyscus maniculatus*. The omega males as a result probably had only brief and irregular access to food. That may have con-

TABLE IV. Males of the Experimental Colonies

	Trapped	Lab wild	Domestic
Intolerant behavior	High	Low	Almost absent ²
Two types of males distinguished by growth	In all colonies	None	In one colony
Mortality (%)	61	2	5
Body weights	Reduced (alphas and betas excepted)	All reduced	All increased ²
Adrenal weights	Much increased (alphas and betas excepted)	Increased	Unaffected ²

²Except one colony.

tributed to their loss of weight and to other ill effects. Such consequences of irregular meals have been observed in laboratory rats by Welker et al [1977]. Thus cannot however account for the loss of weight of the lab wild males for their movements were not restricted by an alpha. In the colonies of domestic rats (RwL excepted) there was no evidence that the movements of any rat were restricted in this way. Both the lab wild and the domestic rats (except in one colony) were nonterritorial.

In the wild colonies there was a distinction between the alphas and betas on the one hand and the omegas on the other. The former differed from the omegas not only in their behavior and increase in body weight but also in the weights of their adrenals which resembled those of the controls. Adrenal hypertrophy represents a physiologic response to adverse external conditions. In that sense it may be called an index of stress [Vogt 1954]. Only the omegas of the wild rat colonies had greatly enlarged adrenals; their adrenal weights resembled those of the attacked wild rats described by Barnett [1958b]. In this early work the attacks were by males resident in a large cage and were directed at strange males (intruders). The behavior (reviewed by Barnett [1975]) is described in detail. It is still not known whether adrenal hyperactivity in such conditions is adaptive. Except in colony RwL, there was no evidence of adrenal hypertrophy in any of the domestic rats.

The exceptional colony (RwL) though an isolated instance is methodologically important. Even in a closed breeding stock there was sufficient variation for one of six colonies to differ decisively from the rest. Evidently the difference arose from the presence of a single male that behaved rather like a wild male. We do not know the proportion of such males in this (or any other) strain or whether its difference from the others was genetically determined. The existence of such males in varying proportions in different domestic stocks could account for conflicting experimental findings.

Another significant methodologic observation concerns the lab wild rats. Barnett et al [1969] reported results of breeding wild *R. norvegicus* for six to nine generations in the laboratory. Attack time and the incidence of the arched back threat posture recorded in standard conditions were greatly attenuated. In our experiments even two generations in the laboratory had measurable effects. The pattern of social interactions in the lab wild colonies was more like that of domestic rats than that of the trapped wild rats; mortality was lower among the trapped rats and adrenal hypertrophy was slight or absent.

Price [1978] has compared trapped *R. norvegicus* with the first generation bred in captivity. The encounters were each between a resident adult male and a strange intruder. The trapped males threatened much more than the first generation males. His findings therefore conform with ours and as Price states they suggest that the laboratory environment is a major source of the differences observed. Price [1977] also gives evidence that male wild *R. norvegicus* of the

first generation reared in the laboratory are less likely to make burrows than are males trapped in the wild domestic rats burrow even less. His findings suggest that the laboratory environment reduces the propensity to burrow but that the difference of domestic from wild in this respect is mainly genetically determined.

There is evidence of variation in the rates over generations in captivity at which different kinds of behavior alter. There is marked difference between wild and domestic rats in the avoidance of unfamiliar objects in a familiar place or neophobia [Barnett et al 1976] but unlike the social interactions described in the present paper neophobia persists for at least twelve generations in captivity [Cowan 1977]. Furthermore, Price et al [1977] observed the maternal behavior of wild and domestic (albino) females at several stages after parturition and found little difference.

The lability of the intolerant behavior of wild rats illustrated by our findings is not confined to *R. norvegicus*. J. L. Carstairs (unpublished observations) has made similar observations on *R. villosissimus*. Trapped males have been compared with males of the first generation reared in the laboratory: those reared in captivity were slower to attack and threatened less than the trapped males. His animals were taken from exceptionally dense, probably still growing populations and they may therefore have been genetically unusually diverse but the extent to which genetic differences influenced his findings is not known. Rigorous experiments are needed on both the genetic and the environmental factors responsible for such changes.

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Aggression, Crying and Physical Contact in One-to Three-Year-Old Children

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In a longitudinal study in which 59 first-born middle class children were observed in the company of other children of the same age and with their mothers a high frequency of attacks on other children by children nearly two years old was correlated with absent or delayed response by the mother to the child's crying after falls etc. Other aspects of mother's or child's behaviour were examined but all failed to explain away this correlation. Some routes by which the correlation could have arisen from immediate influences of the child's behaviour upon the mother were also excluded. Thus it was not true that "tough" kids fight a lot and stop crying quickly. Nor did mothers respond less to children who cried often.

Key words: peer-peer interaction mother-child interaction aggression crying attachment

INTRODUCTION

Most research on aggressive behaviour in animals concerns the causes and consequences of normal aggressive behaviour. In contrast this paper like much other research on aggressive behaviour in children concerns individual differences. Interest in child development traditionally centres on explaining the extremes of normal variation. We think the distinction is important: explanations of abnormal aggressive behaviour and of individual differences in aggression could be very different.

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from explanations of the occurrence and development of normal aggressive behaviour Smith and Connolly [1974-1978] have conducted a series of studies of environmental factors that influence the rates of aggression in preschool children as a whole. Patterson and colleagues [1973-1974] on the other hand have carried out an important series of studies on troublesome levels of aggression in children and Manning *et al* [1978] carried out an important study of individual styles of aggression. This paper follows in the latter traditions to the extent that it concerns correlates of individual differences in aggression and examines some hypotheses about the causes of the individual differences.

We want to know why some children show much higher frequencies of aggression than others. By aggression we mean simply the number of occurrences of the following: hits, bites, pulling hair, kicking, pushing another child, taking an object from another child, pulling at an object that another child has. Blurton Jones [1978] and others have shown that these vary together with each other but occur independently of other patterns best labeled "play fighting" or "rough and tumble." Descriptively the behaviour of the few most frequently aggressive children in our sample resembled the "unprovoked assaults" discerned in earlier data on 3-4 year-olds here by Burke (unpublished) and independently described and traced by Manning in children from 4-7. In our experience of toddlers these assaults are noticed by the mother of the aggressive child and are distressing to her. Even in the absence of any firm demonstration of long term consequences, this is reason enough to provoke further investigation of influences upon this behaviour. The behaviour with which we are concerned should not be confused with unruly or hyperactive behaviour which is sometimes called aggressive.

During a longitudinal study of attachment, social behaviour, and language development we noticed that children who were noteworthy for the frequency and style of their aggressive behaviour to other children also had unusual patterns of physical contact with their mothers. We particularly wished to test in our data the impression that crying by the aggressive children less often led to physical contact with mother than in the less aggressive children.

Any observed correlation between parent behaviour and offspring behaviour may be investigated in at least two directions: (1) determining whether the correlation is primarily between these two measures or is more closely between some other associated pair of parental and child measures (see hypotheses 2 and 3 below) and (2) attempting to ascertain the direction of causation, if any, underlying this particular correlation (see hypotheses 4 and 5 below).

Since it is safe to assume that development of a mother-child relationship is a constant process of two-way interaction, and since no statistical technique can be used with these circular relationships, any testable hypothesis about direction of causation underlying a correlation is bound to be an over-simplification. However, a simple causal hypothesis is at least falsifiable. One can test whether a particular hypothesis

can be excluded. The status of causal theories of mother-child interaction is thus exactly like that of any other scientific theory: it generates falsifiable hypotheses but can itself never be proved true. A view that emphasises the total entwinedness of the relationship may feel more true and may even allow empirical prediction from one age to another. But parents believe they have some influence on their children and some control over whether they behave one way or another. They daily ask for advice from health visitors, general practitioners, teachers. If psychology is to improve the empirical evidence behind the advice given, it has either to tell parents that they cannot change their own behaviour because it is part of a totally entwined system of interaction, or it has to risk employing causal models in research. The causal models will at first be too simple, and because they are hypotheses capable of disproof, often wrong. But eventually, and after experimental study, the causal approach may give useful answers. This paper represents a very simple attempt to move towards testing causal models of individual difference on nonexperimental data.

We have examined our data to test the following hypotheses:

- 1) The child's aggression to other children is predicted by slow maternal response to crying.
- 2) This relationship can be explained away by the higher levels of interaction with peers by aggressive children, i.e. it is not specific to aggressive behaviour.
- 3) That other features of the maternal behaviour, particularly more severe punishment, are more closely correlated with higher aggression, and account for the correlation with response to crying.
- 4) That slow maternal response to crying may be found in children reported by their mothers to have never liked physical contact (like those described by Schaffer and Emerson [1964a]) and that these were also the aggressive children.
- 5) That the persistence or frequency of the child's crying might explain the maternal response, and its association with aggression (i.e. tough children cry briefly and fight a lot; soft children cry long enough to get a response and don't fight).

One thousand and one other hypotheses have not been tested.

SAMPLE

Sixty firstborn children (fathers' occupations in Registrar General's Social Classes I and II) were recruited through health visitors in three North London boroughs. The sample comprised 34 boys and 25 girls, first children of white British mothers and fathers. There were no twins. No mothers in full-time employment were recruited. Many were working part-time or worked more as the study proceeded. There were no children in single-parent families, and no second children had been born in the families when the study began.

METHODS

The first observations and interviews took place when the children were 15 months old and continued at 6 month intervals thenceforth. Children and their parents were seen in a variety of carefully chosen situations for a total of about 2½ hours interview and 2½ or 3 hours observation at each age. The measures used in this paper are described below. The observations that provided the data reported here were at 15 months, 21 months and 39 months and were from three group visits to the playroom at the Institute of Child Health at each age. Each visit lasted about 2 hours. Four mothers and their children would come together to the playroom and a nursery nurse was present for most of the session. The mothers had coffee and orange juice after about 40 minutes and after a further spell of unstructured time a specially arranged separation was arranged between two of the mothers and children in succession. The data analysed for this paper come from 10 minutes of observation of each child during the initial unstructured period and 10 minutes from the second unstructured period, a total of 40–60 minutes for each child at each age depending on how many sessions the child attended.

Behaviour was recorded with pencil and paper as a string of two-letter codes corresponding to previously defined small observable items of behaviour or people. Each verb (behaviour code) had an actor and recipient associated with it. Distances and positions were recorded as verbs. A time mark was put in the record every 10 seconds in response to an automatic sound signal to the observer. The method of observation was derived from that of Leach [1972] and the rationale of this kind of observation was described by Leach and by Blurton Jones [1972a, 1976b]. Observer reliability was good for the more frequent items recorded. The key behaviour with which this paper is concerned is very infrequent and it is scarcely practical to do the usual kind of reliability test. Consequently we have treated the observers as an additional independent variable and examined their effect on the findings. Two regression analyses are shown in Table III. In each analysis one of the three observers is taken as a dummy variable and is entered first in the equation to see whether the central association that we report is really due to observer effect. There is no influence of observer.

Mothers were interviewed at home at each age about a variety of topics concerning their child. This included questions about punishment and questions about attachment used by Schaffer and Emerson [1964b] and from these and other questions we sought information about the child's like or dislike of physical contact with mother. Another section concerned with the mother's description of her child's behaviour covered physical contact.

THE MEASURES

In this paper we are concerned with a few measures, some of which need a careful definition.

DELY (15 Months and 21 Months)

Maternal responsiveness to cry and arms up refers to the time from a record of the child beginning to cry or doing arms up (see below) to a record of the mother picking up the child onto her lap or into contact with her body. We did not count putting an arm round the child, leading it by hand, standing it up onto its feet, putting it onto a piece of apparatus or furniture. Time was assessed in two ways. Firstly by the number of behaviour codes in the record that intervene between the cry and the pick up. An upper criterion was set of 24 codes. This represents nearly half a minute, and there were virtually no cases in which if no pick up occurred within this time it occurred subsequent with no further record of cry or arms up. Most instances involve either an extremely rapid pick up (within 2-4 codes and well within the same 15 second block in the observation) or no pick up at all. The second measure of delay was the number of times mother picked up the child with in two 15 second time marks in the record from the start of crying. The two measures correlate with each other very closely ($r = 0.903$ $P = 0.001$).

Episodes of cry and pick up are rare, and one would expect the measure to be very inconsistent. However, the correlation between the 15 month scores and the 21 month scores was moderately high and statistically significant ($r = 0.363$ $P = 0.005$).

In our sample the responsiveness to cry was not related to frequency of crying episodes. Thus one cannot argue that responsiveness was directly determined by the frequency of the child's crying (eg. mother stops responding because the child is in a bad mood and cries so often, or eg. mother responds rapidly because it is unusual for her child to cry).

There is some evidence that crying that persists ie. the child does not stop crying within 15 seconds, is more likely to get a response. However, this is not an inflexible influence on mother response. In an analysis of this measure of response to crying we found that persistent criers could receive either the slowest or the fastest responses depending on the mother's earlier history.

Consequently we feel that our measure is worth working with, containing a large component of variation due to differences between mothers rather than differences between the child's immediate behaviour. We think it is important to discriminate between immediate effects of the child's behaviour and long term effects. An example of the latter is the likelihood that mothers learn how readily their child stops crying with and without picking up.

AVDLY

A combination of DELY15 and DELY21. If DELY15 was available for a child but there were no DELY21 (21 months old) data available, then AVDLY was equal to DELY15. Likewise, if only 21 month data were available, AVDLY was equal to DELY21. If data were available for both ages, AVDLY was $(DELY15 + DELY21)$ divided by 2.

MUTC

Frequency with which mother speaks to child during the group observations

MAPC

Frequency with which mother holds an object towards the child during the group observations

MRN (Mother's Verbal Responsiveness to Vocalisations)

From the solitary observations the proportion of child vocalisations (that were not crying, fretting, laughing or imitations of vehicles, animals etc.) that led immediately to mother speaking to child (but not with a prohibition). This measure of responsiveness is not correlated with DELY, our measure of responsiveness to cry.

PICKING UP AS A CONSEQUENCE OF AGGRESSION

The observation data for the 15 months observations and the 21 months observations was searched for episodes in which the child attacking or taking things from another child was followed within one minute by mother picking up the child. This is the only measure of the consequences of the child's aggression that we have examined.

PCAS21 (at Age 21 Months)

Percentage of behaviour items directed to other children that were aggressive items (ie hits, bites, push, pull at an object in another's hand, take object put before the other releases the object and without the other proffering the object).

AGG21

Number of aggressive items (see above) performed by the child in one hour of observation.

PCF

Percentage of records of distance between mother and child which are of more than 4 feet. Records of child in physical contact with mother are included and count as less than 4 feet.

SOC 15 (At Age 15 Months and SOC 21 at Age 21 Months)

Number of times in one hour of observation that child speaks, smiles, approaches or proffers to other children.

Obstetric History

The number of minor obstetric problems (from the list given by Prechtl (1961)) during the mother's pregnancy and delivery reported by the mother during the

by item interview (This measure correlates Spearman's rank order correlation = 0.65 $P < 0.001$ and 0.59 $P < 0.001$) with two independent codings of reports direct from the hospitals.)

Punishment

Children were classified using the interview data according to whether the mother said she ever smacked the child or not (70% smacked at 15 months 81% at 21 months) and whether she ever used punishments such as removing the child from the room where she was or confining it to its bedroom (6% at 15 months 19% at 21 months).

Cuddler or Non Cuddler

Children were classified according to the mother's interview comments concerning physical contact in two separate parts of the interview. Seven children were classified as resisting or disliking physical contact with mother.

RESULTS

Hypothesis 1

Aggression at 21 months is correlated with slow response to crying at 15 months and at 21 months (Table I). Aggression at 39 months is associated with the combined 15 and 21 month response to crying (ADVLY) (medians test $X^2 = 4.0$ $P < 0.05$). This hypothesis is mainly confirmed.

Hypothesis 2

Aggression at 21 months is correlated with amount of other social behaviour to children and with average distance from mother (Table II). Children who are far from their mother and are often interacting with other children also show more aggressive behaviour. This hypothesis is therefore realistic.

TABLE I Spearman Rank Correlation of Aggression (AGG21) and Percentage of Social Behaviour That Is Aggression (PCAS21) With Delayed Response to Crying at 15 Months (DELY15) at 21 Months (DELY21) and From Both Ages Combined (ADVLY)

	DELY15	DELY21	ADVLY
AGG21	$r = 0.311$ $P = 0.035$	$r = 0.328$ $P = 0.023$	$r = 0.351$ $P = 0.011$
PCAS21	$r = 0.487$ $P = 0.007$	$r = 0.420$ $P = 0.005$	$r = 0.492$ $P = 0.001$

TABLE II Spearman Rank Correlations of Aggression (AGG21 PCAS21) and Response to Crying (DELY21) With Child's Social Behaviour to Peers (SOC21) Distance From Mother (PCF21) and Frequency With Which Mother Speaks to Child (MUTC21)

	SOC21	PCF21	MUTC21	MAPC21
AGG21	$r = 0.625$ $P = 0.001$	$r = 0.540$ $P = 0.001$	$r = -0.276$ $P = 0.037$	$r = 0.123$ $P = 0.016$
PCAS21	$r = 0.074$ $P = 0.312$	$r = 0.335$ $P = 0.012$	$r = -0.395$ $P = 0.004$	$r = 0.164$ $P = 0.136$
DELY21	$r = 0.070$ $P = 0.338$	$r = 0.178$ $P = 0.143$	$r = -0.291$ $P = 0.039$	$r = 0.1$ $P = 0.046$

However slow response to crying is not correlated with social behaviour or distance from mother (Table II). When forced into a stepwise multiple regression the measures do not remove the relationship between responses to crying and aggression (equations 1 and 2 Table III).

Aggression measured as a proportion of all social behaviour to peers (PCAS) is also correlated with response to crying (Table I). Thus mothers who respond slowly or not at all to crying have children in whom a higher proportion of their behaviour to peers is aggressive. This hypothesis is thus disproved. In our data response to crying relates specifically to aggression and not to all interaction with peers.

Hypothesis 3

There is no correlation of aggression with the punishments reported by the mother. There is also no correlation of aggression at 21 months with the mother's readiness to respond to the child's vocalisations by speaking to the child when mother and child are alone. The latter is closely related to language development, IQ scores and verbal and object exchange interactions with mother and less closely to responses to strange adults [Blurton Jones et al. in preparation]. There is a negative correlation between aggression at 21 months (PCAS21) and the frequency with which the mother speaks to the child and proffers objects to the child in the situation (Table II). Again one has to examine the role of the distance between mother and child in these associations. When distance is entered first in a regression equation predicting aggression (equation 6 Table III) the associations with mother speaks is reduced but does not disappear. This is in direct contrast to the association between aggression and response to crying (equation 5). Equations 8 and 10 show that if DELY21 is taken into account MUTC21 has no influence whereas the reverse is not true. Equations 3 and 7 show that MAPC21 has no influence whether distance or DELY are taken into account. To this extent we can say that response to crying is the feature of maternal behaviour most related to aggression in this age group.

TABLE III Summary Statistics of Regression Analyses Described in the Text

Equation number	Dependent variable	First independent variable	Cumulative R squared	Second independent variable	Cumulative R squared	Overall significance
1	ACC21	PCI21	22.4%	DLLY21	79.2%	$F = 7.21$ $P = 0.002$
2	ACC21	SOC21	57.2%	DILY21	64.5%	$F = 31.8$ $P = 0.000$
3	PCAS21	MAPC21	4.7%	DLLY21	18.8%	$F = 4.05$ $P = 0.026$
4	PCAS21	DLLY21	17.6%	MAPC21	18.8%	$F = 4.05$ $P = 0.026$
5	PCAS21	PCI21	8.9%	DLLY21	23.0%	$F = 5.23$ $P = 0.010$
6	PCAS21	PCI21	10.8%	MUTC21	17.1%	$F = 4.45$ $P = 0.017$
7	PCAS21	PCI21	10.9%	MAPC21	11.7%	$F = 2.69$ $P = 0.079$
8	PCAS21	MUTC21	11.8%	DILY21	22.7%	$F = 5.13$ $P = 0.011$
9	PCAS21	DLLY21	17.6%	MUTC21	22.7%	$F = 5.13$ $P = 0.011$
10	PCAS21	Observer 1	0%	DILY21	17.6%	$F = 3.74$ $P = 0.034$
11	PCAS21	Observer 3	2.8%	DILY21	22.5%	$F = 4.09$ $P = 0.011$

Expressed as percentage of variance accounted for

The child's attacks on other children were only seen to lead (in the following minute) to the mother picking up the child on 16 occasions. Thus in such a minute proportion of both the attacks and the picking up episodes that we can scarcely test and cannot claim any support for our suspicion that the very aggressive children were reinforced by obtaining a significant proportion of their physical contact with mother as a result of attacks on children.

Thus hypothesis 3 was disproved with respect to the measures mentioned above but of course these measures do not comprise every conceivable measure of parental behaviour.

Hypothesis 4

Seven mothers clearly described their child as not cuddly or not enjoying physical contact. The remarks of a further two suggested that their child could be satisfied in this way. There was a nonsignificant tendency for these mothers to have responses to crying. These children did not differ from the others in their scores on aggressive behaviour. This hypothesis was therefore not confirmed.

Hypothesis 5

As we reported elsewhere [Blurton Jones et al 1978] crying persists more in children with sub-optimal obstetric histories (using the criteria of Prechtl [1970]). Also their mothers tend to respond more rapidly and often to crying. But these children are neither more nor less aggressive than optimal children at 15 and 39 months of age.

Categorising the children directly on their scores for persistent crying tells the story. For example there is no difference in the proportion of persistent crying at 39 months between the children who show any aggression to peers at 39 months and those that do not. The hypothesis that the correlation between aggression and maternal response arises because tough children fight more and cry less persists is not confirmed. There is no support for the more general hypothesis that the obstetric history of the child leads separately to different response to crying and to usual levels of aggression.

DISCUSSION

We observed that mothers who picked their child up after a delay or not at all after it began to cry or put its arms up had children who more often attacked other children. We showed that this correlation was specific to aggressive behaviour and was not general to all kinds of interaction with peers. We showed that the relation was with mother response to cry and arms up rather than with observed maternal vocal and gestural behaviour or punishment as reported by the mother during interview.

Nonetheless we feel that the hypothesis that features of mother other than these are closely related to aggression needs further study. It is really a large family of hypotheses. Interview reports of punishment may be inadequate and features of observable behaviour that we did not analyse may be important especially further aspects of the mother's responses to the aggressive episodes.

We examined two hypotheses that explained the observed correlation as a result of features of the children and excluded them. No doubt many others remain to be defined and tested. Many other hypotheses about the correlation of response to crying and frequency of aggression have not been tested. Much variation in the factors influencing the mother's response to crying has been ignored. Since crying is such infrequent behaviour it is likely to be more productive to follow our findings with experimental studies with the cooperation of mothers of aggressive toddlers rather than by yet lengthier and yet more detailed observations.

Even if the correlations that we observed do reflect an influence of the maternal behaviour at this age upon the child, the question remains open as to whether the maternal behaviour at this age was in turn influenced previously by features of the child. We have discussed the influence (contemporary and long term) of the more persistent crying of the obstetrically sub-optimal children. Elsewhere [Blorton Jones et al in preparation b] we describe an interaction between the mother's own family history and the child's obstetric history in predicting the mother's response to crying and arms up. We have commented that children reported by their mother as never having liked to be cuddled tended to get slower response to crying and arms up. However we do know that some of these few children were cuddly with their father or sat comfortably on our laps on occasion. It is by no means clear how the non-cuddly category develops but of course the mother's classification of her child as non-cuddly could either lead her not to pick it up or it could simply be a rationalisation of her reluctance to pick it up. One major possible influence that we have not examined is the speed with which the child stops crying after it is picked up. Moss [1967] presented indirect evidence that this was an influence on the response of mothers to crying.

We know that several of the children markedly changed their frequencies of aggressive behaviour from age to age. Despite an overall continuity some individuals changed markedly. The same is true for the mothers in both directions. Thus although Manning also finds individual consistency in styles of aggression in children from 4 to 7 years old it would be wrong to regard this as an irreversible feature of a 1-3 year-old child's behaviour. Indeed elsewhere we shall present the evidence in our data that the consistency of the child's behaviour can be explained by the consistency in the mother's behaviour rather than vice versa.

Very few studies have observed children of this age with their mothers and with other children. We are thus unable to find anything comparable to our results in the literature. The nearest is the observation by Montagner [1978] and Montagner

et al [1978] that aggressive-dominant children (noted for their frequent aggression and infrequent sociable behaviour) had mothers who interacted with them with few of the facial expressions and gestures classified by Montagner as "appealing" (eg smile head on one side proffering objects). He also found the child's behaviour to change with the mother's behaviour in her economic or social circumstances changed. Main [1973] argued that children with unresponsive mothers showed hostility to their mothers in the Ainsworth "strange situation" procedure as if they failed to disperse tension without their mother's help. Prescott [1971] has argued that lack of physical contact should be related to aggression including unprovoked aggression but was unable to locate direct examples for children's behaviour. Our findings though unique and thus much in need of replication do not stand in complete isolation.

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Evidence That Resident Male Albino Rats Are Not Immune to Attacks by Conspecific Intruders

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Offensive behaviors were exhibited by adult intact and castrated male Sprague Dawley rats introduced into established home-cages of male conspecifics. Implications of this result for Adams [1976] model of intraspecific fighting are presented.

Key words: rats intraspecific fighting resident intruder paradigm

INTRODUCTION

"Territoriality" commonly is defined with reference to agonistic behavior. Territorial animals are ones which occupy and defend an area; they repel members of their species by means of attacks and/or displays [Mover, 1968; Wilson, 1975]. Most species of territory-occupying animals usually are safe from attack by a conspecific intruder so long as they remain in their own home region.

Rats occupying an area (such as a burrow or laboratory cage) reportedly are safe from attacks by a conspecific intruder. Numerous studies demonstrated that male rats defend their home regions from unfamiliar male conspecifics by exhibiting full aggressive posture and biting attack [Adams, 1976; Blanchard and

Blanchard 1977 Calhoun 1962 Lehman and Adams 1977 Luciano and Lor 1975 Price 1978 Telle 1966 Thor and Flannelly 1976] Territory inhabiting rats never were attacked by conspecific intruders [Adams 1976 Thor and Flannelly 1976]

We now report that territory occupying male albino rats are not immune to attacks by conspecific intruders. The present investigation originally was designed to determine how frequently resident male albinos attack male castrated and ovariectomized conspecific intruders [after Thor and Flannelly 1976]. However, we obtained the unpredicted finding that intruders initiated fights with residents rather than vice versa. Subsequently a follow up experiment was conducted to examine this unexpected phenomenon more closely.

EXPERIMENT 1

The first experiment was designed as an analysis of agonistic behaviors exhibited by Sprague Dawley albino rats. Essentially the study was a replication of a previous one dealing with agonistic interactions between Long Evans hooded resident rats and conspecific intruders of different hormonal statuses [Thor and Flannelly 1976]. Since unselected male albino rats allegedly do not fight very often [Bar 1960 Conner 1972] we attempted to maximize the likelihood of eliciting agonistic behaviors by 1) conducting test sessions during the animals' dark phase, 2) using the resident intruder paradigm, and 3) housing the resident rats in isolation for several weeks prior to testing.

METHOD

Subjects

Forty-eight sexually naive rats of the Charles River CD strain purchased from the Charles River Breeding Laboratories were used. Twenty-four were intact males, 12 were castrated males, and 12 were ovariectomized females. Gonadectomies were performed when the subjects were 30 days of age. Like sex pairs of rats were housed in wire mesh cages (18 X 25 X 20 cm) with a reversed 12-hour light-dark cycle and food and water available ad libitum.

Procedure

Twelve of the intact males were selected randomly and designated as residents. They were transferred to larger wire mesh cages (28 X 28 X 34 cm) at 10 days of age and housed individually for 7 weeks prior to the start of the experiment. Residents could not see or contact each other. The 12 castrated males (group C), 12 ovariectomized females (group OV), and the remaining 12 intact males (group I) were designated as intruders. They were maintained individually in wire mesh cages (18 X 25 X 20 cm) kept in a room separate from that housing resident rats.

When all subjects were about 120 days old intruders were introduced into residents' cages on 3 alternate days. Every resident was exposed to three intruders, a different one from each intruder group, one per day. Every intruder was exposed to only one resident. Intruder-resident pairings were arranged according to a schedule counterbalanced for order. A 25 W red incandescent bulb was the sole source of illumination during testing, which was conducted several hours after onset of darkness [after Kane and Knutson 1976]. All intruders, regardless of group, were marked identically on their tails. This permitted the experimenters to distinguish between residents and intruders while remaining blind to intruders' experimental conditions. The experimenters used electromechanical counters to record frequencies of the following behaviors exhibited by residents or intruders during the first 20 minutes after intruder introduction: 1) sniff anogenital region, 2) rub against cage, 3) nosing, 4) attack (and latency to first attack), 5) full aggressive posture, 6) offensive side posture, and 7) full submissive posture [Grant and Mackintosh 1963]. The observers also recorded the number of ultrasonic vocalizations emitted during resident-intruder pairings. Rats' calls were monitored with an ultrasound detection device (Psysonics Inc., Binghamton, New York) sensitive to 20–25 kHz frequency range [after Lore, Flannelly, and Farina 1976; Sales 1972].

Intruders were removed from residents' cages 21 hours after introduction. Each intruder was asphyxiated with ether, shaved, and its skin examined for wounds. Experimenters recorded the number of small (less than 0.5 cm), medium (between 0.5 and 1.0 cm), and large (greater than 1.0 cm) wounds. A wound score was calculated for each intruder [after Luciano and Lore 1975]. Intruders' stomachs were exposed and examined for ulcers [after Lore and Luciano 1977].

RESULTS

The behavioral, wound score, ultrasound, and ulcer data were analyzed using analyses of variance. The statistical tests revealed a significant difference between residents' reactions to groups I, C, and OVX for only one dependent measure – anogenital sniffs ($df = 2$ and 22 , $F = 7.01$, $P < 0.005$). Group OVX intruders were sniffed most frequently ($X = 16.0$), group C intruders were sniffed next most frequently ($X = 11.9$), and group I intruders the least frequently ($X = 8.8$). This result is consistent with that previously reported for Long Evans rats [Thor and Flannelly 1976].

Unexpectedly, several intruders exhibited offensive behaviors (i.e., full aggressive posture and biting attack [Grant and Mackintosh 1963]) during the 20-minute observation period. Attacks by intruders were observed in as many as four pairings, three including group I intruders and one including a group-C intruder. Full aggressive postures by intruders were seen in as many as ten pairings, five including

group I rats and five including group C rats. None of the group-OVA intruders showed attack or full aggressive posture.

Investigators who previously used a resident intruder paradigm to study fear by rats reported that intruders never exhibited attack (e.g. Adams 1976). But the findings of previous research were that territory-occupying rats 1) initiated fights with conspecific intruders and 2) were immune to attacks by conspecific intruders. Since the results of Experiment 1 were contrary to those of other experiments, we attempted to replicate and study in greater detail attacks initiated by intruder rats.

EXPERIMENT 2

METHOD

Subjects

Sixteen experimentally naive rats of the Charles River CD strain born and reared in the laboratory were used. Eight were intact males and eight were intact females. After weaning at 25 days, like sex pairs of rats were housed in wire mesh cages ($18 \times 25 \times 20$ cm) with a 14/10 hour light/dark cycle and food and water available ad libitum.

Procedure

Four of the males were selected randomly and designated as residents. Each of the four males was transferred to a larger wire mesh cage ($65 \times 25 \times 18$ cm) at approximately 140 days of age and housed alone for ten days. Then two 90-day-old females were introduced into every cage. Each set of male and females was allowed to cohabit for ten days prior to testing. Previous research showed that cohabitation with females promoted agonistic activity exhibited by male Lewis rats (Flannelly and Lore 1977). All females were removed from colonies at two hours daily and kept in holding cages as an attempt to adapt the females to the procedure of removal.

The remaining four males were designated as intruders. They were maintained individually in wire mesh cages ($18 \times 25 \times 20$ cm) kept in a room separate from that housing resident rats. Intruders were approximately the same age as residents.

Intruders were introduced into colony cages on the 11th day after cohabitation. Females were removed from each cage approximately ten minutes prior to intruder introduction. Every resident was exposed to only one intruder and every intruder was exposed to only one resident. Testing for resident intruder agonistic encounters was conducted according to the procedure of Experiment 1 except that no attempt was made to monitor ultrasounds.

RESULTS AND DISCUSSION

The findings of Experiment 1 were confirmed: offensive behaviors were exhibited by intruders during the 20-minute observation period. Attacks and full aggressive posture by intruders were seen in two pairings. The sequence of behaviors exhibited by one of these two pairs was particularly interesting. After introduction into the colony cage, the intruder began to sniff and ambulate around the cage. The resident shortly thereafter approached the intruder and sniffed his anogenital region. Cage sniffing by the intruder and anogenital sniffing by the resident continued for a minute or two, interspersed with bouts of nosing [contact between the snouts of the two rats; Grant and Mackintosh 1963]. Subsequently, the resident pursued the intruder (while the latter ambulated around the cage) and repeatedly sniffed his anogenital region. Pursuit was followed by multiple mounts, thrusts, and autogrooming of the genitals. The resident mounted the intruder numerous times until finally the intruder turned and attacked the resident. Not only did the intruder display biting attack and full aggressive posture, but the resident exhibited full submissive posture [lying on back with paws up in the air, exposing the ventral body surface; Grant and Mackintosh 1963]. The resident was observed making slow, continuous exhalations, which previous research showed were correlated with 22 kHz ultrasonic vocalizations [Lore et al. 1976]. Attacks were initiated by the intruder on 3 occasions during the 20-minute observation period; on each occasion, attack was preceded by persistent mounting of the intruder by the resident. Consequently, the resident exhibited full submissive posture as many as nine times in total. A similar sequence of behaviors was exhibited by the other resident-intruder pairing in which attacks by intruder were seen.

The results of the present investigation are contrary to those previously reported by investigators who used a colony intruder paradigm to study fighting by rats. The results of previous experiments were that intruders never attacked colony males, and that colony males never exhibited full submissive posture [Thor and Flannelly 1976]. Moreover, Adams [1976] model of intraspecific fighting does not predict offensive behavior by intruders. According to that model, offensive behavior ordinarily follows the olfactory comparison between a familiar environment and a strange male rat. Intruder rats used in both of the present experiments displayed offensive behavior in a situation where the environment was strange. Thus, presumptive odorant(s) of a familiar environment were not a necessary factor for eliciting attacks by albino rats. Adams' model probably would be more general in its application if 1) the hypothesized comparison were between a strange male conspecific and an attacker's own odorant, and 2) it took into account nonolfactory attack provoking acts, such as repeated homosexual mounting.

Resident rats used in the present investigation exhibited very low frequency

and intensity of agonistic behavior. This finding is consistent with that of another study of fighting which used unselected albino rats [Barnett 1960]. Evidently there are differences between strains of domestic rat since investigators who experimented with Long Evans hooded rats reported vigorous fighting by the resident animals [eg Price 1978]. There also appear to be differences between test paradigms since investigators who studied attack behaviors of male members of mixed sex albino-rat colonies reported vigorous fighting by their homecage animals [eg Blanchard and Blanchard 1977]. Parametric experiments designed to assess the importance of strain and test paradigm as factors affecting offensive interactions would be very helpful for identifying the independent variables related to onset of attack.

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Adrenal Mediation of Intermale Aggression Maintained by Aromatized and Reduced Metabolites of Testosterone

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Individually housed CD-1 mice were either sham castrated or castrated and treated with testosterone (T), estradiol benzoate (EB), dihydrotestosterone (DHT), a combination of EB and DHT (EB+DHT), or the injection vehicle. Following 16 days of isolation and subcutaneous injections, animals were tested repeatedly for fighting behavior in paired encounters with nonaggressive stimulus males. Results indicated that the T and EB+DHT groups fought to the same extent as the gonadally intact group. Both the EB and DHT groups fought more than the vehicle-treated group but less than the T, EB+DHT, and sham castrated groups. A similar study was subsequently performed with adrenalectomized animals. Adrenalectomy eliminated agonistic responses in animals receiving metabolites of testosterone (EB, DHT, EB+DHT) but had only slight effects in gonadally intact and T-treated castrated mice. The results suggested that a) EB and DHT, either singly or in combination, maintain aggression through a synergism with adrenal steroids; b) the combined effects of EB and DHT reflect an additive action rather than synergistic interaction, notwithstanding the synergism with adrenal steroids; c) metabolism of testosterone to estrogen and dihydrotestosterone does not sufficiently account for the action of testosterone.

Key words: testosterone, estradiol, dihydrotestosterone, adrenals, aggression, isolation.

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INTRODUCTION

Simple endocrine manipulations such as castration and testosterone replacement have established androgen-dependencies for intermale aggression in male and male copulatory behavior in rats. In a series of remarkably parallel studies of sexual and aggressive behavior, compelling evidence has been gathered to suggest that the maintenance of these responses is also dependent upon the active metabolism of testosterone by neural tissue.

It is evident that testosterone metabolism occurs in the brain. Following the *in vivo* administration of ^3H testosterone, the bulk of radioactivity in rat brain cell nuclei consists of three components: estradiol 17β formed by aromatizing enzymes in the brain; dihydrotestosterone formed by reducing enzymes in the brain; and unmetabolized testosterone [Lieberburg and McEwen, 1977]. Similar metabolic processes occur in brains of other species, including the mouse [Naftolin and Ryan, 1975]. Moreover, both the rat and mouse possess a specific brain receptor for estrogens and an androgen receptor which binds dihydrotestosterone and testosterone [Attardi and Ohno, 1976]. Behavioral evidence is consistent with the hypothesis that testosterone metabolites mediate testosterone action. Exogenous combinations of estradiol and dihydrotestosterone maintain sexual behavior in the castrated rat [Baum and Vreeburg, 1973; Larsson, Soderstrom, and Beyer, 1973] and intermale aggression in the castrated mouse [Brain and Poole, 1976; Finney and Erpino, 1976]. Although most of the data suggest that estradiol and dihydrotestosterone interact synergistically to maintain sexual behavior, some studies indicate that estradiol alone is at least as effective as testosterone in maintaining fighting [Bowden and Brain, 1978; Brain and Bowden, 1978; Brain and Poole, 1976]. The results of treatment with estrogen antagonists and aromatization inhibitors further support the idea that testosterone action is dependent upon aromatization. CI 628, a synthetic anti-estrogen which blocks tissue uptake of ^3H -estradiol and inhibits estradiol-induced lordosis behavior [Whalen and Gorzalka, 1973], also impairs testosterone-maintained copulatory behavior in male rats [Luttrell, 1975]. Another anti-estrogen, MLR 25, suppresses androgen-maintained fighting in male mice [Brain, Benton, Goldsmith, and Bowden, 1976]. Steroidal inhibitors of aromatization block testosterone-maintained mounting behavior [Christensen and Clemens, 1975] and intermale aggression [Bowden and Brain, 1978], however, they fail to suppress estradiol-induced behavior and thus appear to have a relatively specific mode of action.

Although substantial evidence supports the speculation that aromatization mediates the effects of testosterone, there is some question as to whether this sufficiently accounts for the observed data. Adrenalectomy eliminates copulation in castrated rats maintained with either high doses of estradiol [Gorzalka, Reiter, and Whalen, 1975] or low doses of estradiol in combination with dihydrotestosterone [Gorzalka and Roach, 1978]. In contrast, adrenalectomy fails to affect

copulatory activity in testosterone treated castrates. Since estradiol treatment often increases adrenal secretion rate [eg Colby and Kitay 1976] and produces considerable adrenal hypertrophy and hyperplasia when combined with dihydrotestosterone [Gorzalka and Roach 1978] adrenal steroids such as androgens, estrogens or glucocorticoids may act in concert with exogenous estradiol and dihydrotestosterone to maintain copulatory behavior. Thus the ability of estradiol and dihydrotestosterone to maintain ejaculations can be interpreted as evidence for aromatization, adrenal stimulation or both. The present study examined the relative effectiveness of androgens and estrogen in maintaining intermale aggression in castrated and adrenalectomized castrated mice.

EXPERIMENT 1

Both testosterone and a combination of estradiol and dihydrotestosterone can restore fighting in castrated mice [Brain and Poole 1976, Finney and Erpino 1976]. However, there is some question as to whether estradiol alone restores agonistic behavior or whether dihydrotestosterone synergistically facilitates the action of estradiol. In castrates of the Tuck TO strain, normal levels of fighting are maintained with either 25 μ g testosterone (T), 1 μ g EB, estradiol benzoate (EB) or a combination of 500 μ g dihydrotestosterone (DHT) and 1 μ g EB [Bowden and Brain 1978, Brain and Poole 1976]. Treatment with EB in the absence of DHT also restores fighting in castrated Swiss Webster mice [Edwards and Burge 1971]. In contrast, even massive doses of EB fail to appreciably restore aggression in castrated CD 1 mice [Luttge 1972]. In the latter strain, restoration of preoperative levels of aggression apparently requires either 500 μ g T or a combination of 2-4 μ g EB and 200 μ g DHT [Finney and Erpino 1976]. These diverse results likely reflect differences in techniques for generating intermale aggression as well as strain differences in sensitivity to steroids analogous to those previously reported for sexual behavior in mice [Gorzalka and Whalen 1974, 1976]. The present study attempted to confirm that EB and DHT act synergistically to maintain intermale aggression in CD 1 mice.

METHODS

CD 1 male were obtained from Canadian Breeding Farms, Montreal, Canada and were housed in groups of six per cage with food and water available ad libitum. Animal colonies were maintained at 21°C on a 12/12 hour light/dark cycle with lights on at 2200 hours. At the age of 60 days, animals were either castrated ($N=60$) or sham castrated ($N=12$) while under light ether anesthesia. Mice were individually housed in 11 (height) \times 28 \times 16 cm polypropylene cages immediately after surgery. These were equipped with straight wire tops, each of which contained a built-in feeder and water dispenser which together displaced 452 cc. At

the age of 64 days daily subcutaneous hormone injections were started. Ca received either 500 μ g T ($N=12$), 4 μ g EB ($N=12$), 200 μ g DHT ($N=12$), 4 μ g combined with 200 μ g DHT ($N=12$) or the oil vehicle. 0.05 ml of peanut oil. Sham castrates received the oil vehicle.

Behavioral tests were conducted on the 16th, 18th, and 20th injection day. Stimulus CD-1 males which had been housed 6 per cage served as opponents in test bouts. Test sessions were conducted between 1300 and 1600 hours in Plexiglas enclosures measuring 22 (height) \times 12 \times 23 cm. Tests were conducted in neutral enclosures rather than home cages to permit comparison with the work of Finney and Erpino [1976]. Each experimental male was adapted to the enclosure for 5 minutes, presented with a stimulus male, and observed for 10 minutes. Experimental stimulus male pairings were randomized for successive test observation periods; the latency to attack and the frequency and duration of attacks against stimulus males were scored via an Esterline Angus event recorder. This permitted statistical analysis of the following measures: percentage of animals that fought at least once, percentage of trials in which fights occurred, mean number of attacks per trial, mean cumulative attack duration per trial, mean attack duration per attack (calculated by dividing cumulative attack duration by number of attacks for each animal), and the mean latency to attack. Animals which failed to attack were assigned a latency of 600 seconds.

RESULTS

As shown in Figure 1, treatment with either T or a combination of EB and DHT (EB+DHT) maintained intermale aggression at levels comparable to those exhibited by intact animals. Treatment with either EB alone or DHT alone appeared more effective than vehicle treatment. Fisher exact probability tests [Siegel, 1956] indicated that there were no significant differences between the T, EB+DHT, and intact groups on the percentage of trials with attacks. All three groups differed significantly from the EB group ($P < 0.001$), DHT ($P < 0.001$), and vehicle group ($P < 0.001$) on the percentage of trials with attacks. While the vehicle group exhibited less trials with attacks than the DHT ($P = 0.003$) and EB groups ($P = 0.010$), the two steroid groups did not differ from each other. There were no significant differences between the T, EB+DHT, and intact groups on the percentage of animals fighting at least once. Intact animals and T treated castrates were more likely to fight than either EB treated ($P = 0.007$) or vehicle treated castrates ($P < 0.001$) but not DHT treated castrates. The EB+DHT group did not differ from the EB-treated ($P = 0.033$) and vehicle treated group ($P < 0.001$) but not the DHT group. DHT treatment was significantly different from vehicle treatment ($P = 0.006$) although the percentage of EB treated animals attacking did not differ from that of either DHT treated or vehicle treated animals. Table I summarizes that comparable differences occurred in the number of attacks per trial, cumulative attack duration per trial, and attack latency. An analysis

variance revealed significant differences in the mean number of attacks ($P < 0.01$). Group comparisons were made using a posteriori Newman Keuls tests at the 1% probability level. This indicated two homogeneous subsets: one consisting of the T, EB+DHT, DHT and intact groups and the other consisting of the vehicle, EB

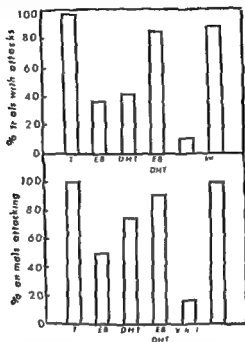


Fig. 1. Effects of steroid hormone treatment on the percentage of CD-1 mice attacking at least once in three successive tests and on the percentage of trials with attacks. Animals were castrated and treated daily with T (N=12), EB (N=12), DHT (N=12), EB+DHT (N=12) or the oil vehicle (N=12) or had intact gonads and were vehicle treated (N=12).

TABLE I. Effects of Steroid Hormone Treatment on Intermale Aggression in Castrated CD-1 Mice*

Treatment	N	Mean number of attacks per trial	Mean cumulative attack duration (sec) per trial	Mean attack duration (sec) per attack	Mean attack latency (sec) per trial
T	12	91 ± 14	310 ± 45	36 ± 03	1203 ± 438
DHT	12	39 ± 09	138 ± 33	34 ± 08	4269 ± 930
EB	12	28 ± 16	99 ± 38	38 ± 07	4068 ± 618
EB + DHT	12	82 ± 13	240 ± 33	32 ± 04	2196 ± 683
Vehicle	12	17 ± 07	44 ± 13	29 ± 05	5421 ± 184
Intact gonads	12	70 ± 11	230 ± 27	39 ± 05	1914 ± 717

*Results are based on the mean (± standard error) of three successive tests.

and DHT groups. An analysis of variance and Newman Keuls comparisons revealed an identical pattern of significant treatment differences in the mean cumulative attack duration per trial. However, there were no significant differences in the mean duration of attacks. An analysis of variance indicated that there were no significant differences in mean attack latency ($P < 0.01$). Newman Keuls comparisons revealed two homogeneous subsets: one consisting of the T, EB+DHT, EB, DHT, and intact groups and the other consisting of the EB, DHT, and vehicle groups.

EXPERIMENT 2

The results of Experiment 1 confirmed that combined treatment with EB and DHT mimics T in maintaining preoperative levels of agonistic behavior in the CD-1 mouse. It remains to be determined whether the combined action of the testosterone metabolites was mediated by adrenal stimulation. If adrenalectomy were shown to differentially influence T-treated and EB and DHT-treated animals, this would suggest that aromatization of T to E and reduction of T to DHT do not sufficiently account for testosterone action. This design rests on the assumption that adrenalectomy per se would not suppress intermale aggression in intact mice. The literature is controversial on this issue although at worst fighting is merely reduced and not abolished by adrenalectomy (Brain, Howell, and Wou 1971; Harding and Leshner 1972). Some investigators contend that adrenalectomy has no effect (Burge and Edwards 1971; Welch 1968; Yen, Day, and Sigg 1966). It has been suggested that adrenalectomy does not produce a lasting suppression but prolongs the isolation interval required for the development of intermale aggression (Sigg, Day, and Colombo 1966). Because of this suggestion, the present experiment employed previously isolated and experienced animals. The effects of adrenalectomy on intact mice and steroid-treated, castrated mice were examined.

METHODS

On the day following the last behavioral test in Experiment 1, all experimental animals were bilaterally adrenalectomized while under light ether anesthesia. Body and adrenal weights were recorded. Adrenalectomized mice were subsequently maintained on 0.9% saline. Daily injection schedules identical to those of Experiment 1 were continued. Similar behavioral tests were conducted on the 14th and 16th postadrenalectomy days. In order to minimize the influence of nonspecific debilitation, behavioral data were excluded from analysis if animals failed to survive to the 37th postadrenalectomy day.

RESULTS

As shown in Figure 2, only T-treated castrates and gonadally intact mice continued to fight after adrenalectomy. Although the EB+DHT group was not

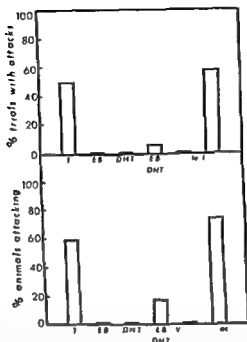


Fig. 2. Effects of steroid hormone treatment on the percentage of adrenalectomized CD 1 mice attacking at least once in three successive tests and on the percentage of trials with attacks. Animals were castrated and treated daily with T (N=10), EB (N=7), DHT (N=6), EB+DHT (N=6) or the oil vehicle (N=8) or had intact gonads and were vehicle treated (N=8).

to the T and intact groups prior to adrenalectomy, all but one animal in the group failed to fight after adrenalectomy. That animal fought on one trial only. Fisher exact probability tests indicated that there were no significant differences in the percentage of trials with attacks between either the gonadally intact and T groups or the EB+DHT, EB, DHT and vehicle groups. Both the gonadally intact and T group animals fought on more trials than the EB+DHT ($P < 0.001$), EB ($P < 0.001$), DHT ($P < 0.001$) and vehicle groups ($P < 0.001$). There were no significant differences in the percentage of animals fighting at least once between either the intact and T groups or the EB+DHT, EB, DHT and vehicle groups. Intact animals were more likely to fight than EB+DHT ($P = 0.048$), EB ($P = 0.006$), DHT ($P = 0.009$) and vehicle treated animals ($P = 0.003$). T treated animals were more likely to fight than EB ($P = 0.017$), DHT ($P = 0.026$) and vehicle treated animals ($P = 0.011$).

Table II reveals essentially the same pattern: gonadally intact and T treated animals fought, others did not. Since agonistic responses were frequently absent, nonparametric tests were used to analyze the data in Table II. On three of the measures—number of attacks per trial, mean cumulative attack duration per trial

TABLE II Effects of Steroid Hormone Treatment on Intermale Aggression in Adrenalectomized Castrated CD 1 Mice*

Treatment	N	Mean number of attacks per trial	Mean cumulative attack duration (sec) per trial	Mean attack duration (sec) per attack	Mean attack latency (sec) per trial
T	10	4.9 ± 1.3	16.5 ± 3.4	2.9 ± 2.1	780.4 ± 94.9
DHT	6	0	0	0	600.0 ± 0
EB	7	0	0	0	600.0 ± 0
EB + DHT	6	0.7 ± 0.7	1.8 ± 1.8	2.5 ± 0	560.5 ± 31.6
Vehicle	8	0	0	0	600.0 ± 0
Intact Gonads	8	4.8 ± 1.1	12.6 ± 3.5	2.7 ± 1.1	344.3 ± 11.3

*Results are based on the mean (± standard error) of three successive tests

and mean attack latency statistical differences between groups were identical. Mann-Whitney U tests [Siegel 1956] indicated that T was more effective than EB+DHT ($P < 0.05$), EB ($P < 0.05$), DHT ($P < 0.05$) and the vehicle ($P < 0.05$). On the same measures, gonadally intact mice were superior to castrates treated with EB+DHT ($P = 0.015$), EB ($P = 0.007$), DHT ($P = 0.010$) and the vehicle ($P = 0.005$). There were no significant differences between either T-treated castrates and intact mice or EB+DHT, EB, DHT and vehicle-treated castrates. The fourth measure in Table I, mean duration of attacks, was not statistically analyzed since the number of attacks was commonly zero.

It is apparent that postadrenalectomy scores were lower than preadrenalectomy scores. This is best illustrated by comparing the percentage of trials in which fighting occurred in the present experiment with the percentages of the corresponding animals in Experiment 1. McNemar tests for the significance of changes [Siegel 1956] revealed postoperative reductions in castrates receiving T ($P < 0.001$), EB+DHT ($P < 0.001$), EB ($P < 0.025$), DHT ($P < 0.01$) and gonadally intact mice ($P < 0.025$).

An analysis of variance of adrenal weights revealed no significant differences. However, there was a trend toward differences between the intact group and each of the castrate groups. Mean adrenal weights (mg) and standard errors were as follows: T 5.3 ± 1.1 , EB+DHT 5.5 ± 1.4 , EB 5.2 ± 0.8 , DHT 5.5 ± 1.0 , vehicle 5.0 ± 0.9 , intact 3.6 ± 0.4 . Adrenal/body weight ratios presented essentially the same patterns since there were no significant body weight differences.

DISCUSSION

The failure of EB+DHT to maintain intermale aggression in adrenalectomized mice implies that aromatization and reduction, while perhaps necessary, are not sufficient to account for testosterone action. There are several lines of evidence

which would even challenge the necessity for aromatization. Treatment with dihydrotestosterone, a nonaromatizable androgen, occasionally restores aggression in castrates of some strains [Bowden and Brain 1976; Brain and Poole 1975; Luttge and Hall 1973]. Although previous attempts have failed to find significant effects of dihydrotestosterone in CD-1 mice [Finney and Erpino 1976; Luttge 1972], the steroid clearly facilitated aggression in Experiment 1. Apparently this is the first successful demonstration that a nonaromatizable androgen potentiated fighting in CD-1 mice.

Also, contrary to the aromatization hypothesis, there is a significant negative correlation between agonistic behavior and the activity of aromatizing enzymes in mouse brain cell nuclei [Dessi-Fulgheri, Lucarini, and Lupo de Prisco 1976]. This finding is puzzling in relation to evidence that an aromatization inhibitor blocks T-induced fighting [Bowden and Brain 1978]. There are other inconsistencies in the evidence supporting the aromatization hypothesis. For example, the anti-estrogen MER-25 inhibits androgen-induced aggression in mice [Brain et al. 1976] and facilitates androgen-induced mounting in rats [Baum and Vreeburg 1976]. MER-25 has a mild affinity for estrogen receptors in the mouse and rat brain [Attardi and Ohno 1976]. Baum and Vreeburg [1976] have suggested that since MER-25 and estradiol both have an affinity for brain estrogen receptors and estradiol is normally involved in the control of mounting behavior, MER-25 may facilitate mounting by activating these binding sites. If this explanation were correct, it would suggest that either MER-25 must have a different mechanism of action in the mouse or the action of MER-25 in the mouse is evidence against the aromatization hypothesis. Perhaps the terms aromatization inhibitor and anti-estrogen impart a generous degree of specificity to the drugs they describe.

Aside from the issue of aromatization, there is also reason to doubt Finney and Erpino's [1976] conclusion that EB and DHT interact synergistically. Figure 1 and Table 1 indicate that EB and DHT were individually capable of facilitating aggression to a significant extent and therefore may have simply acted in an additive manner when combined. Thus it is conceivable that an increased dose of either steroid would mimic the effect of T. Experiment 2 suggests that the effectiveness of EB and DHT, whether they act synergistically or additively, is dependent on the adrenals. Similarly, when DHT or EB are administered individually, potency is enhanced by the presence of the adrenals. If a synergism exists, it may be between EB and adrenal steroids and DHT and adrenal steroids.

The present results provide further evidence for remarkable similarities in steroidal regulation of intermale aggression in mice and copulatory behavior in male rats. Previous work showed that both behaviors could be activated by either testosterone, estradiol, or a combination of estradiol and dihydrotestosterone. It now appears that unlike testosterone, estradiol or estradiol combined with dihydrotestosterone acts in concert with adrenal steroids to maintain behavior. A variety of treatments purported to facilitate copulatory activity by a direct

action on the brain may be adrenally mediated [eg Gorzalka et al 1975 Gorzalka and Roach 1978 Paris Resko and Goy 1971 Whalen Neubauer and Gorzalka 1975] The same may hold true for intermale aggression

There are some indications of qualitative differences in the steroidal regulation of these behaviors Adrenalectomy per se often produces no significant effect on the copulatory behavior of gonadally intact rats and mice [Bloch and Davids 1968 Wallis and Luttge 1975] In group-housed mice adrenalectomy may even facilitate mating activity [Gorzalka and deCatanzaro 1979] However according to some previous reports [eg Brain et al 1971 Harding and Leshner 1977] and the present study intermale aggression in intact mice is somewhat reduced by adrenalectomy This is not to infer that adrenal hormones necessarily have a permissive action in gonadally intact mice Brain et al [1971] have suggested that the elevated levels of ACTH which follow adrenalectomy rather than the withdrawal of adrenal hormones may directly suppress aggression

Another apparent difference is seen in dihydrotestosterone effectiveness The nonaromatizable androgen restores intermale aggression to at least some extent in castrated mice [Brain and Bowden 1978 Brain and Poole 1976 Luttge and Hall 1973 Experiment 1] However dihydrotestosterone has little or no effect in restoring copulatory behavior in castrated rats [Baum and Vreeburg 1973 Laessle et al 1973] This could merely reflect a peculiarity of the rat rather than a major endocrine difference between mating and aggression In castrated rabbits guinea pigs mice hamsters and rhesus monkeys [Agmo and Sodersten 1975 Alsina and Goy 1974 Luttge and Hall 1973 Phoenix 1974 Whalen and DeBold 1974] nonaromatizable androgens such as dihydrotestosterone partially or completely restore mating activity

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Canine Responses to Familiar and Unfamiliar Humans

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Dogs were observed during controlled approaches by their owners and by strangers. Significant differences between the dogs' responses to their owners and their responses to strangers were found. These results supported the popular belief that dogs respond differently to different persons and not merely to different situations in which persons are usually encountered.

Key words: canids, communication, defense, sociability

INTRODUCTION

The literature on dog-human relationships has long assumed that domestic dogs behave differently toward familiar and unfamiliar human beings. To familiar humans, they are thought to direct affiliative behavior patterns; to unfamiliar humans, patterns of aggression or defense. The phenomenon is interesting because it represents the transfer during the course of domestication of aggressive and affiliative patterns from an intra- to an interspecific context [Fox, 1968, 1971; Fuller and Dubois, 1962; Lorenz, 1952; Schenkel, 1967; Scott, 1958, 1967; Scott and Fuller, 1965].

While often described in anecdotes, this difference in the behavior of dogs toward familiar and unfamiliar humans has never been evoked under controlled conditions. Consequently, the difference might as reasonably be attributed to the different circumstances under which dogs usually encounter familiar and un-

familiar people as to the difference in familiarity. The experiment reported here was designed to discover if the response difference is still observed when dogs approached under standardized conditions.

METHOD

The method was based on John [1973]. Dogs were approached in a standard manner while they were chained in their owners' yards. Each dog was approached once by his owner and once by an unfamiliar experimenter. The dog's behavior during the approaches was filmed and tape recorded.

Subjects

The subjects were 20 dogs, 10 males and 10 females, kept as pets in the city of Worcester, Massachusetts. Subjects ranged in age from nine months to six years. A variety of moderately large to large breeds were used, all with erect

Procedures and Equipment

During the setting up of the experiment, the dog was confined out of sight of the house or kennel. The experimenter's car was parked on the edge of the yard in the best spot for filming and recording and the camera and microphone were positioned inside the car. The camera used was a Beaulieu 8000S Super 8 and recording equipment consisted of a Panasonic microphone attached to a Paraflex RQ-4135 cassette tape recorder.

The procedure called for the stimulus persons to approach the chained dog by walking along the edge of the roadway to a point abreast of the dog, and then turning to walk directly into the yard to a point 16 feet short of the dog. The positioning of the dog and the size of the approach course were varied with the size of the property to keep the proportions as constant as possible. The metal screw-type dog stake to which the dog would be chained was placed from 10 to 50 feet from the edge of the yard. The three stakes which marked the approach course were placed as follows. Beginning at the dog stake, the experimenter walked on a line perpendicular to the street. Stake No. 3 was placed along this line 16 feet from the dog stake and stake No. 2 was placed where the line intersected the edge of the street. Stake No. 1 was placed along the edge of the yard approximately where a person walking along the edge of the roadway would first be noticed by the dog.

The dog was then brought out and attached to the stake by a 10 foot metal chain. The owner and the stranger were hidden down the street from stake No. 1 in a spot out of sight of the dog stake but within sight of the experimenter. When the dog had become acclimated to the situation, the cameraman's

the first approach. When the dog had stopped reacting to the first approach and resumed his preapproach behavior, the cameraman signaled the second approach. The order of the approaches — owner first or stranger first — was alternated from dog to dog.

The approach was regulated by tape recorded instructions played to the approacher through earphones from a cassette tape recorder which the approacher carried over his or her shoulder. Each approach consisted of six movements. During the first movement, the approacher walked from his hiding place to stake No 1 and then along the edge of the yard to stake No 2. At stake No 2, he stopped, turned to face the dog and said "Good dog" in a neutral tone of voice. During the second movement, the approacher walked from stake No 2 to stake No 3, stopped, repeated "Good dog" and waited without moving for approximately ten seconds. During the third movement, the approacher raised his arm rapidly over his head, took a step forward as if to strike the dog, then immediately returned to his previous stance and position and waited for another ten seconds. During the fourth movement, the approacher knelt, saying "Good dog" and extended one hand forward, palm up and open as if to feed the dog. He then returned to his previous stance and position and waited without moving for about seven seconds. During the fifth movement, the approacher turned to face stake No 2. He remained standing thus, with his back to the dog, for about ten seconds and then walked to stake No 2. During the sixth movement, the approacher passed stake No 1 and walked along the edge of the yard past stake No 1 to the spot where he had started.

Data Analysis

The film record was analyzed using an Angus Dual Eight 2808 editor viewer. Forty-two behavior categories were scored for each eight frames (one second) of each movement of the approach. Many of the original categories produced data which were either unreliable, unaffected by experimental procedures, or too low in frequency to warrant discussion. On the frequencies of each of the remaining 19 behavior categories, three analyses of variance were performed to determine 1) if the frequency of occurrence differed during the various movements of the owner approach and during the various movements of the stranger approach, 2) if the frequency of occurrence over all movements of the stranger approach was different from the frequency of occurrence over all movements of the owner approach, and 3) if the pattern of response to the stages of approach differed between the owner approach and the stranger approach. Details of category definitions, reliability figures and variance analyses may be found in Rappolt [1976], a copy of which may be obtained by writing the authors.

BLE I Croup Means

Mean proportion of time X 100

Behavior category	Owner approach					Stranger approach				
	Far ap		Near ap		Mean	Far ap		Near ap		Mean
	proach	speak	proach	speak		proach	speak	proach	speak	
situation	Arm raise	Kneel speak	Back to dog	Exit	Mean	Arm raise	Kneel speak	Back to dog	Exit	Mean
forward	54	60	60	46	57	56	49	40	36	48
intermediate	6	0	72	28	23	19	22	24	26	21
back	06	08	08	06	07	14	16	15	16	14
situation direction										
in motion	74	63	81	75	73	70	66	70	70	69
moves toward	14	15	05	08	09	05	08	04	06	09
moves away	04	08	11	00	09	16	17	12	08	11
horizontal gaze direction										
looks toward	67	65	58	62	60	43	37	31	39	43
looks almost	2	24	19	21	21	19	23	21	21	21
toward	10	07	09	08	12	21	22	18	21	18
looks to side	05	01	12	07	06	16	16	23	12	15
looks away	37	2	14	28	23	19	25	27	29	25
if position	55	7	80	67	72	70	64	57	55	63
down	14	49	16	11	28	21	16	08	05	12
if motion	80	47	78	84	67	70	73	81	84	78
moving	44	30	44	46	37	35	37	47	52	46
still	17	35	77	75	37	38	35	30	32	33
arms	11	14	04	17	15	07	08	02	05	06
forward	31	30	34	37	33	17	17	08	04	12
up	11	11	1	07	03	17	17	08	04	12
down	11	11	1	07	03	17	17	08	04	12
if position	31	30	34	37	33	17	17	08	04	12

TABLE II Significance Levels Analyses of Variance

Behavior category	Between movements within each approach		Between owner and stranger approaches	
	Owner approach	Stranger approach	Approach totals	Patterns of response over stages of approach
Position				
Forward	-	-	$P < 0.10$	-
Intermediate	-	-	-	-
Back	-	-	-	-
Motion direction				
No motion	-	-	-	-
Moves toward	$P < 0.05$	$P < 0.01$	-	-
Moves away	-	$P < 0.10$	-	-
Horizontal gaze direction				
Looks toward	-	$P < 0.01$	$P < 0.01$	-
Looks almost toward	-	-	-	-
Looks to side	$P < 0.05$	-	$P < 0.05$	-
Looks away	$P < 0.10$	$P < 0.10$	$P < 0.01$	-
Tail position				
Up	$P < 0.01$	-	-	$P < 0.10$
Down	$P < 0.05$	-	-	$P < 0.01$
Tail motion				
Moving	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.05$
Still	$P < 0.01$	$P < 0.01$	$P < 0.10$	-
Ears				
Forward	$P < 0.01$	$P < 0.01$	-	-
Up	-	-	-	-
Down	-	-	$P < 0.10$	-
Back	$P < 0.01$	$P < 0.01$	-	-
Bark rate	-	$P < 0.01$	$P < 0.05$	$P < 0.01$

RESULTS

The most frequent response of the dogs during the procedures of the experiment was to stand motionless and silent with head up and tail down and still orienting in the direction of the approacher. Frequent alternative patterns included tail wagging and raising, barking, averting the gaze, and alternately coming toward and rushing back from the approacher.

Some behavior patterns were clearly more common during the close movements of the approach than during the distant movements; others less common. Tail wagging, putting the ears back, looking away, lowering the tail (owner approach) and barking (stranger approach) were all more frequently observed when the

approacher was within the boundaries of the yard (movements 2-5) than when he was outside the boundaries (movements 1 and 6). Holding the tail still pointing the ears forward and holding the tail up (owner approach) were all more frequent when the approacher was outside the boundaries.

Some systematic differences were observed in the patterns of responses of dogs to their owners and to strangers. The dogs gazed at their owners more than at strangers particularly in the early phases of the approaches. They spent more time close to their owners, wagged their tails more for their owners and barked at them less. Although the overall frequency of tail raising was comparable in the two approaches, the temporal course of this response differed. During the stranger approach, the frequency of tail raising remained at a stable, moderate level. During the owner approach, however, the response was more frequent when the owner was at a distance and less frequent when the owner was near.

A surprising feature of the dogs' response to the stranger approach was the combination of barking and tail wagging. Both responses occurred more frequently during the closest movements of the stranger approach than during the distant movements. Direct study of the film record showed that dogs often barked and wagged their tails at the same time. A correlation coefficient computed across dogs shows that those dogs which barked at the strangers most were also those which wagged their tails most ($r = 0.569$, $P < 0.01$).

DISCUSSION

The results lend some support to the idea that dogs differ in their responses to familiar and unfamiliar humans. The owner approached dogs by moving toward the approacher, lowering and wagging their tails and retracting their ears conformed to the pattern of active submission which several authorities agree characterizes the response of dogs to dominant, familiar conspecifics [Scott, 1967 describes the pattern most clearly]. The stranger approached dogs behaved more ambiguously. In some respects their response seemed a less vigorous form of active submission. They too tail wagged, approached and ear retracted to some degree. But in at least two respects their response seemed a different kind of pattern. When the stranger was close, the dogs did not lower their tails and they did bark. Barking has been characterized as belonging to a pattern of defense against threat [Scott and Fuller, 1965]. If this characterization is appropriate, then the dogs in our study were simultaneously giving out appeasing and defensive communications toward the stranger.

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The Development of Territorial-Induced Intermale Agonistic Behavior in Albino Laboratory Mice

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Male mice of the CF 1 strain (*Mus musculus*) were allowed to take up lone residence in a small territory consisting of a 60-cm enclosure attached by a tubular runway to a standard mouse cage with food, water, and bedding. A group of ten mice, each of which resided in its own separate enclosure for 24 hours, were more aggressive toward intruders than other groups of ten mice following six-hour residence periods, or no such residence. Aggression toward intruders increased in repeated weekly tests of the six-hour residents, but after four weeks of testing did not reach the maximum stable level displayed by the 24-hour residents over four weeks of testing. In another experiment, the 24-hour residence period of groups of 20 CF 1 male mice was disturbed by briefly removing the mouse from the enclosure before introducing the intruder at various intervals prior to testing. Removal of the resident five minutes before testing resulted in a marked decrease in aggression toward intruders. Although lesser decreases in aggression followed intervals of 30, 45, and 60 minutes, a 180-minute interval resulted in no appreciable effects compared to undisturbed controls. It is concluded that exposure to the stimuli provided by the enclosure results in an aggressive readiness in the resident mouse which reaches a high level within a 24-hour period.

Key words: aggression, mice, territorial behavior, enclosure, residence period, intruder.

INTRODUCTION

Male mice are known to form territories in large [Anderson and Hill, 1965; Reimer and Petras, 1967] and in small complex enclosures [Crowcroft, 1966; Mackintosh, 1970; Poole and Morgan, 1976]. In either case, the dominant

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male emerging as a territory holder patrols the territory and attacks intruders which cross its boundaries. It has been noted that this behavior should not be interpreted as defense of the territory [see Moyer 1972]. However the cues provided by a small complex enclosure result in a characteristic behavior pattern of intermale aggression in which the resident animal has a decided advantage. The work of Mackintosh [1973] has demonstrated that the cues in the enclosure which delimit the territory of a particular male mouse are primarily visual.

Although a number of variables have been investigated which appear to be necessary for this sort of agonistic behavior, the use of complex enclosures housing several male mice has made it difficult to conduct controlled studies of the behavior itself. A complicated enclosure is not necessary to stimulate the levels of aggression in resident males which is characteristic of the agonistic behavior of territorial males observed in prior studies. Rather than permitting the resident males to determine a territory, each mouse can be placed in an enclosure which is small enough to insure that the resident animal will control the entire area [Thurmond 1975]. Mackintosh [1970] has observed that the behavior of dominant males in control of an entire area shows many of the characteristics of a territory holder in the presence of other males who also hold territories.

The results of prior work [Thurmond 1975] indicated that 90% of resident males attacked and dominated an intruder if the period of residence before testing was at least 24 hours, provided the test for aggression occurred during the active (dark) phase of the animal's diurnal cycle. It had also been observed that although the occurrence of the resident male's agonistic behavior was highly reliable following this period, it also appeared to be vulnerable to disruption in the hour or so just preceding the test. One aim of the present experiments was to investigate the effect of reducing the time spent by the resident in the enclosure before introducing the intruder. The effects of repeating this procedure at intervals of one week for a total of four weeks were also examined. Second, we investigated the degree to which the resident male's agonistic behavior was susceptible to disruption prior to the test for aggression.

MATERIALS AND METHODS

Subjects

Ninety-day-old male mice (*Mus musculus*) of the CF-1 strain (Carter Farms, Wilmington, Massachusetts) were used in the experiments. The mice were housed five per cage on sawdust bedding with Purina Rat Mouse Chow and water available ad libitum. Subjects were maintained on a 12 hour light/dark cycle (lighting 1 PM - 1 AM, fluorescent lighting 1 AM - 1 PM) and all testing was performed under red light four hours into the dark phase of this cycle. Each residence time was marked with a spot of blue liquid food dye to aid in identification. The res-

mouse was challenged with a naive intruder during each test of aggression. A total of 150 residents and 240 intruder mice were used in the two experiments.

Apparatus

The enclosure used for the experiments (Fig. 1) consisted of a 60 cm square box made of 20 gauge sheetmetal. The floor of the box was made of hardware cloth with small 0.6 cm square holes — holes small enough to prevent the mouse from sticking its head through and getting stuck. The box rested on a 65 cm square pan covered first with paper and then layered 1 cm deep with sawdust bedding. The sides of the box were 60 cm high and no top was required to keep the mice from escaping. A tower 30 cm high made of small holed hardware cloth was anchored to the floor of the enclosure and provided an 11 cm square platform at the top for introducing the intruder. When placed in the enclosure on the platform the intruder could climb down the tower to explore the enclosure or the resident could climb up the tower to reach the intruder.

The enclosure was attached via a tube (4 cm in diameter, 12 cm long) to a standard polypropylene mouse cage containing food, water, and bedding. Although displays of aggression may occur in either the enclosure or the home cage, they never occur in the tube; the resident may, however, chase the intruder from one location to the other through the tube.

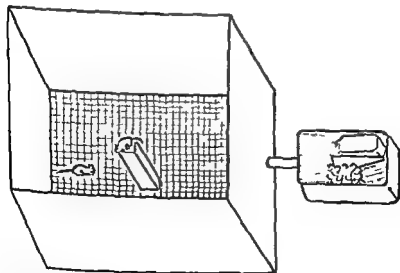


Fig. 1. The experimental enclosure. The box is 60 cm high and is connected by a tube to a home cage containing food, water, and bedding. Note the 30-cm high hardware cloth tower in the center of the box.

Procedure

A complete description of the procedure used for measuring territoriality using the enclosure has been described in a previous paper [Thurmond 1967]. All mice were adapted for two weeks in the laboratory before the experiment began. Two cages, each containing five mice, were transferred to the test room containing five identical territorial enclosures. One cage of mice was randomly designated as residents; then each was marked for identification and placed in its respective enclosure. If the resident mice are placed initially in their home cage, occasionally one of them will fail to enter the enclosure; however, if placed in the enclosure, they always explore it and end up in the home cage. To conduct the test, the five intruder mice were removed from their cages and one was placed in the center of the enclosure box, and the ensuing aggression was recorded during a 30 minute observation period. Observations were made on each pair of mice under the dim red light of the dark cycle. An attack was defined as a bout of activity lasting up to several seconds during which the intruder bit the intruder at least once.

Two experimental procedures were employed. In experiment 1 residents were placed in the enclosures 0 hours (control), 6 hours, or 24 hours prior to introduction of the intruder. In the two treatment conditions, the resident mice were in the enclosure during four hours of the dim (active) phase of the dark cycle before testing. For each of these conditions four repeated tests spaced one hour apart were conducted on the same ten resident males. The residents were removed from the enclosures between tests and regrouped with their cage mates. In experiment 2 all resident mice were in the enclosure for 24 hours before testing for aggression. Groups of 20 residents were removed from the enclosure at intervals of 5, 30, 45, 60, and 180 minutes before aggression testing and then returned immediately to the enclosure. Testing was also conducted on a control group which was not removed from the enclosure.

Parameters recorded during the observation periods were the percentage of residents attacking intruders, latency to attack, and number of attacks.

RESULTS

Experiment 1

The results obtained by changing the period of residence in the enclosure prior to introducing the intruder are given in Table I.

The treatment effects obtained were analyzed by means of two factorial tests of variance with repeated measures on one factor [Winer 1967, pp. 30-31]. The tests of significance were two-tailed. The data of the 0 hour control group show that the number of residents attacking intruders increased from an initial value of 30% during the first test (week 1) to 60% during week 2 but did not increase beyond this value during subsequent tests. When the residents were

TABLE 1 Summary of Agonistic Behavior of Resident Mice Toward Intruders as a function of Period of Residence and Repeated Testing Over a Four Week Experimental Period

	0 hr residential period				6 hr residential period				24 hr residential period			
	Week 1	Week 2	Week 3	Week 4	Week 1	Week 2	Week 3	Week 4	Week 1	Week 2	Week 3	Week 4
	10	60	60	60	60	70	80	80	90	80	90	80
Percentage residents attacking intruder in	Mean 17.3	10.3	8.5	10.6	18.5	14.2	16.2	12.1	11.7	8.3	7.5	7.1
Latency to attack (min)	SEM 1.7	7.8	3.1	2.9	3.6	3.8	4.1	3.6	2.9	3.7	3.4	3.8
Number of attacks	Mean 1.7	7.5	9.0	6.9	18.0	15.9	14.9	15.2	26.1	35.3	24.8	33.9
	SEM 1.0	3.6	4.8	3.5	6.1	5.2	5.4	5.3	6.8	6.3	5.3	6.6

enclosure for six hours before testing, the first time the number attacks the intruder was about 30% below that obtained for the 24-hour residential period, nearly equalled that of the long-term period by the third week of testing. A value of a Chi square test to these differences in the number of residents attacking intruders would be inappropriate here since the groups across weeks of repeated tests are not independent. A comparison of the number of residents attacking intruders during week 1 for each group does not reach statistical significance ($F = 5.00$, NS). However, the systematic increase in the number of residents attacking intruders over the four weeks of testing in the 6-hour group seems a fairly clear indication that these animals became more aggressive. The number of resident males attacking when left in the enclosure for 24 hours prior to testing was stable at 80-90% across the four weeks of repeated testing.

The latencies to attack shown in Table I for the 0-hour and 6-hour residents are longer than those obtained for the 24-hour residents ($F = 7.87$, $df = 3, 12$, $P < 0.05$). Values for this measure generally decreased monotonically as a function of repeated testing in each of the groups, a trend which reached statistical significance ($F = 5.16$, $df = 3, 12$, $P < 0.01$). There was no significant interaction of this variable with the different periods of residence ($F = 0.55$, $df = 1, 12$, NS). The latency values for the 24-hour group averaged 55% of comparable values for the 6-hour group for each week of testing.

A greater number of attacks on intruders (Table II) was influenced by residence as the residential period increased from 0 to 24 hours ($F = 14.77$, $df = 3, 12$, $P < 0.001$). It can be seen that the number of attacks during the first test (week 1) for the 0-hour group was very low and increased during subsequent tests. However, changes in this measure during repeated testing over four weeks were less remarkable than those observed for the latency measure ($F = 1.17$, $df = 3, 12$, NS) although on the average the 24-hour group evidenced an increase of 55% more attacks than the 6-hour group. The interaction of changes in number of attacks over the four weeks with the different residential periods was not significant ($F = 1.29$, $df = 6, 12$, NS).

Experiment 2

Table II shows that the percentage of residents attacking their respective intruders increased as the time interval separating the disruption from the test for aggression increased ($\chi^2 = 15.47$, $P < 0.005$). The effect of removing the resident mouse from the enclosures just five minutes prior to testing resulted in a marked reduction in the number attacking intruders compared to the controls which were not disturbed ($\chi^2 = 8.05$, $P < 0.005$). The reductions in aggression obtained by removing the resident 30, 45 and 60 minutes before the test were essentially identical; the percentage of residents attacking in each of these groups being 40% lower than controls. When the disruption occurred three hours prior to testing the aggressive level of residents returned to that of controls.

TABLE II Summary of Agonistic Behavior of Resident Mice Toward Intruders as a Function of Disruption Prior to Testing (N = 20 residents in each condition)

		Interval prior to testing					No disruption
		5 min	30 min	45 min	60 min	180 min	
Percentage of residents attacking intruders		30	60	65	65	85	95
Latency to attack (min)	Mean	24.0	14.7	15.8	16.7	6.3	6.0
	SEM	2.3	2.8	2.6	2.6	1.4	1.5
Number of attacks	Mean	13.0	26.2	19.6	24.1	29.9	39.5
	SEM	5.5	5.8	4.5	6.5	6.2	4.7

Similar differences between the groups were obtained using the other two measures of agonistic behavior. Group differences were analyzed using a one factor analysis of variance and where significance was obtained it was followed up with a test for comparison between treatment means by the Newman Keuls method [Winer 1962 pp 80-85]. As in experiment 1 all tests of significance were two tailed. The decrease in the latency to attack the intruder as a function of the interval prior to testing was significant ($F = 9.12$ $df = 5, 114$ $P < 0.001$). Comparisons indicated that the 180 minute and no disruption groups differed from the five minute group (Newman Keuls $P < 0.01$) and from the (30-60) minute groups (Newman Keuls $P < 0.05$). Also the five minute group differed significantly from the (30-60) minute groups (Newman Keuls $P < 0.05$).

The increase in the number of attacks on intruders as the interval prior to testing increased (Table II) was significant ($F = 2.63$ $df = 5, 114$ $P < 0.05$). The only comparison yielding statistical significance was between the five minute and the no disruption group (Newman Keuls $P < 0.05$).

DISCUSSION

Previous work [Thurmond 1975, Thurmond et al 1977] had shown that 90-100% of CF 1 males attacked intruders if left in an enclosure for 24 hours prior to testing for aggression. In experiments conducted by Oortmerssen [1970] on the tendency of different strains of mice to fight on their home ground a 24 hour period was also employed which produced aggressive resident males. The results of experiment 1 indicate that males who reside in the enclosure for six hours are less aggressive toward intruders than those left in the enclosure for 24 hours before testing. Thus although six hours would seem to be an appreciable period of residence in the small and relatively simple enclosure used the stimuli associated with the enclosure somehow induce a high level of aggression when the mouse is exposed to them for 24 hours.

Repeated weekly exposure in the case of the six hour residents increased the occurrence of resident attacks on intruders but the latency of attacks and frequency of attacks on intruders did not reach those exhibited by the 24 hour residents. In contrast repeated weekly confrontation of the 24 hour residents with an intruder had no positive effects on the number of these residents' attacks on intruders. This result however was due mainly to the fact that 90% of these residents attacked intruders during the first test leaving little room for increase in this measure during subsequent tests. The measures of latency to attack and frequency of attacks on intruders indicate that aggression in the 24 hour residents tended to increase somewhat during repeated testing. The stimuli in the enclosure for inducing an aggressive readiness to attack intruders are likely to be related to the visual configuration of the enclosure particularly the presence of the tower [Mackintosh 1973] and the odor of urine deposits in the enclosure [Mackintosh and Grant 1966; Ropartz 1965; Dixon and Mackintosh 1971].

Whereas the frequency of occurrence of C57BL male mice attacking intruders is high following 24 hour residence in the enclosure it had been observed in our laboratory that it was also easily disrupted by certain events just prior to testing. Loud noises or flashes of light seemed to leave the resident mouse relatively unperturbed but even slight movements of the enclosure or brief attempts to enter the resident were capable of profoundly decreasing the occurrence of attacks on an intruder. Each of the measures of aggression employed in experiment 1 indicated that removing the resident mouse from the enclosure five minutes before testing reduced aggression toward the intruder to approximately 30% of control (control levels). Resident aggression levels on the average were still 60% of control levels following the same disruption even 1 hour before introduction of the intruder although they returned to control levels when the disruption occurred three hours prior to testing. It is not possible to determine from the results whether the reduction in aggression is due to handling of the resident or to removal of the animal from the stimuli in the enclosure which apparently induce an aggressive readiness during the period of residence. Minor changes in an enclosure just prior to challenging residents with intruders seem to do little to reduce aggression [Mackintosh 1970].

It appears from the results of the present experiments that an aggressive readiness develops in C57BL male mice in the enclosure employed over a 24-hour period in the sense a) that mice left in the enclosure for as long as six hours do not display maximum levels of aggression toward intruders nor were maximum levels reached following four weeks of repeated testing under these conditions and b) that somewhere between one and three hours are required for aggression to return to high levels in residents who are removed briefly from the enclosure near the end of a 24 hour period of residence.

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Book Reviews

Peacekeeping Police Prisons and Violence by Hans Toch Heath
Lexington Massachusetts and Toronto 1976 pp v + 137

Hans Toch's writing is unduly elliptical. As an example: police officers who casually approach men with guns. Who have the guns: the police or the men they approach? The "casually" makes it the police, but the reader has to stop to work it out. Against this the writer sometimes sparkles suddenly. An anything goes view of means has a way of including violence. The wise guy on the beat or the opposing hockey player in a cut throat game may be casually dealt with because it doesn't really matter. A similar stance can justify the rape of inmates and undervalues poetry in report writing. The last sentence stops one short, but this time working it out is illuminating.

Little has so far been written, as Toch remarks, about violence in formal organisations. Rules are one thing, practice is something quite different. It is easy to tell psychiatric attendants that disruptive patients may be restricted or immobilised as a last resort. But what is a last resort? And what are the alternatives to physical restraint? More technical still, since there are more and less violent ways of getting patients into a camisole (here the reviewer in his Scottish ignorance must guess that this is not a flimsy female undergarment), how is the nurse to choose which ways to adopt? A patient curses and lifts a chair, he is large and looks wild, others are restive. There is no time to consult a supervisor or wait for the doctor. An action is taken and a precedent is set.

In police and prison work, as in psychiatric hospitals, policy makers and directors in the background have to think of their executives in the face to face situation. Given the fact that police and prison officers face potentially dangerous situations fairly regularly, since their clientele are violence prone, the organisation has to cope with fear — the fears of their staff as well as the fears of the dangerous clientele. On both sides, be it emphasised, both lots come from social groups which believe that physical prowess and willingness to fight are *measures of manly worth*. The general program of the book is to work out ways of undermining the hold of violence promotive norms grounded in subcultural attitudes so strong as to be accepted without question as the natural law of the situation.

The impression one gets, possibly too hasty, is that everything is still to be done. The American Correctional Association Training Guide lists eighteen duties as com-

prising the work of guard personnel. Of these only one — Hears inmate grievances and counsels inmates — envisages a relationship other than adversary or supervisory between officers and inmates — and it is almost certain to be crowded out by 17 other seventeen rules mostly operating against the provision of time for officer-inmate personal contact. Of course that was in 1959 but a similar handbook in New York State current in the 1970s prohibits the correctional service employee from engaging in any conversation, communication, dealing, transaction, association or relationships with any inmate or former inmate or any visitor, friend

in any manner or form which is not necessary or proper for the discharge of the employee's duties. Against that there are a few initiatives in the direction of mixing. One is the ombudsman idea: there are fourteen prison ombudsmen currently active in the US, ten of them correctional staff members, a device which stimulates inmate scepticism. But in two instances — Minnesota and Connecticut — the ombudsman has promoted staff-inmate consultation and helped to reduce conflict and to relieve tension. In police work the move from law-enforcement to peace-keeping as the main police function is prospering here and there. Toch's brief and detached summary of this development is sobering. His language is consistently hypothetical. In team policing theory the police are brought closer to the community: they can adjust their activities to community needs and can work closely with citizen representatives. If this principle held, the violence reduction potential would be obvious: teen age gang members are not likely to play "wise-guy" football with a man in a yellow blazer who coaches their softball team; riots do not form among spectators to an arrest that is inspired by a community plea voiced in the two nights previously.

In general, the badly needed attitude change is still in the future. What police agencies are not doing is facing their involvements — the full gamut of their involvements — with pride. The organisational reluctance to face service involvements is easily explained. To face a service role means thinking of police as preserving the peace, not as combatting crime. Where agencies — this appears to mean police departments — experiment with service functions, they meet improved public acceptance. Even modest efforts provide citizen esteem. This gives the police a greater sense of security. They are consequently less apt to be trapped into responding to challenges, taunts, baiting and tests of manhood. And with these admirable propositions the book comes to an end.

Toch may be ignoring the more cheerful and sometimes more zany aspects of American prison life. BBC television has just (October 1978) turned out a programme about Fort Worth in which the prisoners are paired off, male and female, so that they may fall in love and so pacify and improve each other. Many of them held that the pairing would probably not survive liberation. The rule was that personal contact while lavish must not occur below bench or waist level. How this is managed was not explained. Toch's omissions are probably deliberate and probably do credit to his good judgment.

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Anger Control by Raymond W. Novaco. Heath, Lexington, Massachusetts and Toronto, 1975. pp. xii + 134.

The appearance of this small book is fitting since, as the author remarks, the problem of human anger and its consequences is assuming substantial importance in developed societies of the 1970s. Novaco's book deals with anger at the psychopathological end of the spectrum. It reports a study designed to evaluate systematically the efficacy of several modes of behavioral psychotherapy in the control of psychopathological anger. In reading the book, this reviewer got the distinct impression of assessing a doctoral thesis or a lengthy journal article. But the material it contains is sufficiently relevant and scientific to justify publication.

The first chapter is a rather selective review of the literature on aggression. While this selectivity is perhaps dictated by the nature of the book, it is surprising that little mention is made of the literature on crowding and aggression, since, though this is often speculative, it seems central to many of the issues of social importance raised in the concluding chapters.

The primary importance of the book, however, lies in the two chapters outlining the design and execution of a study to evaluate methods of anger control. The study was modest: thirty-four subjects took part in the psychotherapeutic programs aimed at controlling extreme anger. In line with much psychological research, subjects were drawn largely from a university population. The statistical design is good.

Criticism can, however, be made of some aspects of the assessment of anger. Novaco makes much of an Anger Inventory, evidently developed for this study. Little is said of the psychometric aspects of its development; no evidence is given, for example, of its validity. In view of the availability of reputable instruments which might have been used to validate it, and in view of the importance placed on the Anger Inventory as a measure of therapeutic change, this is a glaring deficiency. To be fair, other means of assessment are also used, but these measure anger only indirectly.

The therapeutic program provides interesting reading, indeed, especially for clinicians who are increasingly required to help persons with problems of psychopathological anger. It is based firmly on behavioral psychotherapy and particularly on the modification of cognitive activity, an area that should be familiar at least to clinical psychologists. Novaco has dissected the complex issue of anger control in a thoroughly logical way, and therapeutic procedures are explained in admirable detail. Hence clinicians should have little difficulty either in applying them or in

replicating the entire study in a research investigation. Assuming the adequacy of the measurements as valid indices of therapeutic change, the results obtained are impressive and clinically valuable. Whether the value of such a program extends to all the areas mentioned in the concluding chapters — the control of child abuse, aggression among police officers and so on — remains to be seen. It does, however, deserve further examination.

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Cruelty and Kindness by Harvey A. Hornstein. Prentice Hall
Englewood Cliffs, New Jersey 1976 pp vi + 154

The Psychodynamics of Hostility by Leon J. Saul with Barbara
Wrubel Jason Aronson, New York 1976 pp x + 223.

How do you study human kindness? Well, if you are a social scientist, you devise experiments to test how people will respond to money left on the street, lost wallets, or you telephone strangers and ask for help. Then you measure the results: how many people returned the money and wallets, or helped you on the telephone. And you repeat the studies in other cultural contexts. From these kinds of observations, you synthesize a theory of behavior. But can the theory explain altruism, the subheading of the book? Perhaps, but such theories make me uneasy. They grapple with complex human motives, but derive evidence only from contrived, on the street manipulations. I become even more uneasy when similar types of experiments are used to study aggression. The proper understanding of aggression must involve, at some point, a detailed study of the criminal and the victim. Aggression research done with animals or within the setting of the laboratory is very far removed from war and murder and rape. Thus, to extrapolate from the Milgram studies to a general theory of cruelty is a large inference. Yet Hornstein, a psychologist, has done it in this slim paperback, which is somewhat popularized for easy reading. And it does read well, and is interesting. But I kept asking: Is it that simple? I wish it were.

On the other hand, Saul has written a book describing psychoanalytic principles of aggression and clinical mechanisms underlying human behavior. He discusses examples and shows how they conform to intrapsychic mechanisms. Guilt, psychopathology, and psychosomatic styles of coping are mentioned at length. Later in the book, the author talks of love and politics as more elaborate defenses and sublimations concerning rage and hate. I think the reader of this more complex volume will be interested in the intricacies of the unconscious, but no doubt will be perplexed by the theory, which is so inaccessible to the average scientist and clinician. To some extent, Saul's work is the mirror image of Hornstein's: the latter deals only with obvious, overt behavior, while Saul deals with the underlying motives.

and conflicts which give rise to the behavior. Saul switches at the end of the book to psychosocial considerations of violence. He offers ideas for not only the prevention but also the cure for violence. One cure he says is enough love. That of course is always an interesting notion but is the answer also that simple?

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Abstracts of the Third Biennial Meeting of the International Society for Research on Aggression

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HUMAN AGGRESSION A

Chair Ronald Baenninger Temple University Philadelphia

Frances J. Fitch Alan Gold and John R. Lion (University of Maryland Baltimore)

A Group Therapy Experience With Violent Alcoholic Patients

Because patients with violent aggressive behavior often show severe characterologic problems including impulsivity, absence of guilt, and difficulties maintaining stable intimate relationships, they are frequently regarded as untreatable and generate discomfort in practitioners and trainees. Little attention is given to them in allocation of psychotherapy resources or residency training.

This paper describes a group of psychotherapy for violent alcohol abusing patients now in its fourth year. Group work with these patients provides an appre

ciation of the complexity of primitive character pathology increases skill and competent handling of countertransference aspects of their treatment and produces increased interest in and greater comfort with psychotherapeutic work with them.

Problems in establishing a referral base and its ultimate composition are discussed including the screening and evaluation process, criteria for acceptance and the initial therapeutic contract.

The composition (diagnostic, socioeconomic) of the group, patterns of attendance, and typical group sessions (process and content) are described. Important recurrent themes and approaches that have been found useful are enumerated. These include alcohol use by members, impulsive action either out of rage or "proof of masculinity" with little regard for consequences, arrested development with spouses, boisterous aggression to cover over passive feelings for intimacy and warmth, frustration with bureaucracies and mistrust of authorities, common defensive patterns of splitting, denial, and reaction formation. Techniques of therapy are described. Handling of crises by use of the telephone, hospitalization, and occasional discharge from the group are discussed. Demands on therapists by probation officers, lawyers, and courts are described.

Concluding remarks on outcome for patients identify the therapeutic factors responsible for change. Rewards for therapists are described, including the different responses of five therapists who have worked with this group over its four-year existence.

David Student and John H. Lion (University of Maryland, Baltimore)

Methodological Issues in Psychopharmacological Research of Violent Individuals

To date no pure antiaggressive agent has been found. In search for a substance the authors have recently conducted a study of a drug found to have some anxiolytic effects in animals in preclinical investigations.

Although many different pharmacological agents are used in the control of violent patients, they affect the target symptom of aggression only secondarily. The present use of these drug regimens and their rationale are discussed. Theoretically, a psychoactive agent may exist that affects the basic neural mechanisms involved in aggression.

In order to experiment with such a potential antiaggressive drug and test its efficacy on violent patients, an outpatient setting was chosen. The advantages of studying drug effects in the "natural habitat" and of "victim" participation and observation in the experimental design are thus maximized.

Conducting a study of ambulatory violent patients, however, presents numerous problems. Recruitment of reliable patients with high measurable base line of aggression is difficult. Informed consent issues regarding patients on probation precluded their participation. The dual role of investigator as observer and therapist

past and the dynamics particular to this group of patients and their families have to be constantly dealt with

Clinical observations are made of the four patients who successfully completed the eight week experimental period in comparison to the four who dropped out

The authors conclude that despite the difficulties of such a study there is need for further psychopharmacological research in the treatment of violent individuals

Henry Harbin and Denis Madden (University of Maryland Baltimore)

Battered Parents

This paper presents data that identify a new type of family violence problem the battered parent The victims are parents and the perpetrators of the violence are their adolescent and young adult offspring The authors discuss their experience in treating these families and delineate some of the dynamics associated with this type of family violence A primary focus of the presentation is on families in which the parents have been repetitively threatened with physical violence or actually assaulted and who have been unable to stop this established cycle of violence The dynamics of these families appears to be different from the dynamics of families in which child abuse or interspousal violence is the prominent feature

The authors base part of their observations on a research project currently underway that focuses on assaultive adolescents A surprising discovery was that a significant subgroup of these adolescents direct the majority of their aggression toward their parents rather than extrafamiliably as is typical of many delinquent youth A variety of communicational and structural distortions in these families were also noted and summarized in the paper Another striking feature of these families is the manner in which the parents protect these aggressive youths even though the parents are the recipients of the violence The authors have treated a number of these families employing a variety of approaches including family therapy individual psychotherapy and pharmacological approaches In summary the paper attempts to delineate a new syndrome of family violence that has not yet been focused upon in the literature

Heino F. L. Meyer Bahlborg and Anke A. Ehrhardt (Columbia University New York)

Prenatal Hormones and Aggression in Man

This paper reviews the results of studies on human clinical models of abnormal prenatal hormone situations (endocrine abnormalities hormone treatment during pregnancy) and presents new data from a project on the behavioral sequelae of prenatal steroid treatment

Available studies on prenatally masculinized females have documented only statistically insignificant increases in physical or verbal aggression Data from stud

ies on males exposed prenatally to potentially antiandrogenic substances showed slight but significant decreases of aggressive behavior which however may be due to the effects of an abnormal pregnancy as well.

We present data on 15 girls and 13 boys with less severe pregnancy complications who had been exposed to medroxyprogesterone acetate (MPA) in utero and on 28 closely pair-matched control subjects. The double-blind follow-up examination at age 9-13 years involved questionnaires, half-structured interviews with mother and child separately, and a battery of psychological tests. Interviews were tape recorded and rated by two independent raters.

Analysis of the data on aggression shows no differences between experimental and control boys and only some borderline differences between experimental and control girls, with some decreases of aggressive behaviors in the MPA-treated group. We conclude that prenatal hormone effects on human aggression still have not been reliably demonstrated.

Russell E. Monroe (University of Maryland, Baltimore)

Brain Dysfunction in Aggressive Criminals

Ninety-three recidivist aggressive criminals at Patuxent Institution, Jessup, Maryland, were assigned to four subgroups based on the interaction between central nervous system instability and dyscontrol symptoms. Thirty percent of this population could be identified as a group of epileptoid dyscontrol subjects who not only admitted to dyscontrol symptoms on a self-rating scale but also demonstrated evidence of central nervous system instability in the form of drug-induced EEG abnormalities. This group also showed signs and symptoms suggesting mild neurologic disorders and gave a history suggestive of neurologic trauma. They also had a childhood history suggesting the hyperkinetic syndrome. A second group with equal evidence of an EEG abnormality but lacking other neurologic findings and dyscontrol symptoms revealed a severe psychosocial maladaptation that is characteristic of the inadequate personality (psychopath).

A third and fourth group were identified as individuals whose criminality was more determined by psychodynamic or social factors. Although the data were less clear it seemed possible that one group consisted of neurotic or "hysteroid" dyscontrol subjects while the other consisted of pure psychopaths. The data suggest that this classification has specific prognostic and therapeutic implications.

HUMAN AGGRESSION B

Chair Suzanne K. Steinmetz University of Delaware Wilmington

Gordon W. Russell (University of Lethbridge Lethbridge Alberta)

Hero Selection by Canadian Ice Hockey Players Skill or Aggression?

Since the turn of the century studies in which individuals usually children were asked to list the people they admire or most wish to be like have appeared with some regularity. The analyses of such poll type data typically involved percentage comparisons of exemplar types across predetermined categories (eg politicians entertainment science relatives etc). Such investigations have served a useful purpose albeit a limited one in identifying influential societal models and indeed in drawing attention to some fairly important changes in model category preferences during the early decades of this century. The selection of and identification with exemplars was assumed to be made on the basis of one or more attributes held in high regard by the youngsters.

The hockey world has been torn with dissent in recent years over the issue of violence occurring both on and off the ice. Part of the concern has centered on the influence of superstars on the values and behavior of youngsters. Hockey offered an opportunity to quantitatively explore the nature of those bonds with exemplar choices. Weekly cumulative statistics are meticulously kept on all National Hockey League (NHL) teams and players for devotees of the game. Such records thus provide performance indices (goals assists) [Russell 1974] and measures of illegal aggression (penalties).

An approximation of a national sample of attitudes toward young ($\bar{X} = 18.5$ $\sigma = 1.5$) Canadian hockey players ($N = 205$) was obtained on the occasion of the staging of the 1975 Canada Winter Games in Lethbridge Alberta. Subjects were asked to rank-order their favorite three NHL players and team favorites from among those currently active. Regression analyses revealed that team choices were significantly related to their respective performance and aggression standings though more strongly to the former. Individual superstar choices were highly correlated with performance measures but unrelated to aggression.

The subjects also tended to select as exemplars NHL players who play the same position as the respondents. Finally NHL models tended to be selected by subjects from the professional teams operating in the subjects' own Canadian province. The results were discussed within the framework of social learning theory.

Jo Grobel and Dagmar Krebs (Institut für Psychologie Aachen Federal Republic of Germany)

Perceived Situations Anxiety and Their Effects on Aggression

Beside the studies on the effects of violent TV programs on aggression an increasing number of authors draw attention to the effects of these programs on anxiety. In this context Bandura's imitation learning theory does not seem sufficient to explain the development of anxiety. Although an anxious model may be imitated, the perception of a threatening situation shown in fiction or relative aggressive films and a generalization to the actual environment may have an effect on the anxious perception of this natural environment even if the TV program does not show any fear. In our study we were not interested in the immediate fear reactions in front of the TV set associated with physiological arousal and state anxiety but in the development of a cognitive pattern connected with "trait anxiety."

Two dimensions, social anxiety and physical anxiety, seem to be of particular interest in the study of the effects of violent programs as most of the situations shown on TV either induce one or the other. In addition, different characteristics of the watching person (sex, dispositions like neuroticism, experience with similar situations) and of the observed situations (amount of aggressiveness, show reality content, etc.) are interesting. If anxiety appears within the natural environment, this may lead to aggression, as has been reported for social fear.

In a longitudinal field study that ran over three years, an experimental group of 405 children (11-15 years old) was investigated once per year using an anxiety inventory (Aachener Angstfragebogen, consisting of two factors: social anxiety and physical anxiety; factor structure stability over time: 0.98), an aggression scale, and other measures. That there were no measurement effects was shown through the inclusion of control groups, each investigated only once.

Results (based on a hierarchical analysis of variance): Girls reported higher anxiety I and II than boys ($P < 0.001$). High neurotic children had higher anxiety scores than low neurotic children ($P < 0.001$). Children who saw the fictive aggressive films as realistic had higher anxiety scores (I and II) than boys and girls who believed that the aggressive films were unrealistic ($P < 0.05$, no difference for nonaggressive films). The same result was found for a semidocumentary crime serial shown on German TV. Over time there was no significant decrease or increase of anxiety, but the results reported above were reproduced in the three replications. On the basis of multiple regression analysis, anxiety II (social) turned out to be the best predictor (simple $r = 0.40$) for boys' aggression.

So far, it can be concluded that there is a strong relation between the perceived reality content of aggressive films and anxiety, and a strong relation between boys' social anxiety and aggression.

Dagmar Krebs and Joe Groebel (Institut für Psychologie Aachen Federal Republic of Germany)

Confrontation With Aggression in Day-to-Day Life and Its Manifestation in Attitudes Toward Aggression

The considerations and results presented in this paper are based on a longitudinal field study on the effects of television violence on aggression and anxiety in children 12-15 years old

Aggression in our study is not related to behavioral acts of aggression but to attitudes toward aggressive acts. There are three dimensions of attitudes toward aggression empirically established in pilot studies: a) attitude toward destructive aggression, b) attitude toward reactive aggression, and c) attitude toward positively sanctioned or legitimate aggression (eg. violent acts by the police).

In studying television's possibly detrimental effects on the viewer, it seems reasonable to investigate the effects of televised violence not only on open acts of aggression but also on attitudes toward aggression, for the viewer elaborates and evaluates the television diet in the frame of reference of his cognitive system.

The argument is that the viewer may extract behavioral rules from television programs, especially, he may perceive some violent events on television as real and may develop a conviction that conflict resolution or goal attainment by use of aggressive modes of action is highly efficient. It is possible that although this conviction seldom or never leads the viewer to open acts of aggression, it is discovered at the merely attitudinal level.

The central hypothesis is that television viewing is only one, and surely not the most important, part of everyday life influencing the viewer's attitudes toward aggression. There are many other factors and real experiences that may be considered in this context. Presumably, observing violent acts in television is not as concrete an experience as observing violent or aggressive acts in the neighborhood or between peers. Further, being victim of an aggressive act and acting aggressively when alone are even more direct experiences than vicarious experience of violence or aggression in peers or on the television screen.

We suppose that the actual day-to-day experience of a person influences his attitudes toward aggression more than the vicariously experienced violence on television. At least, these daily-life experiences have a mediating effect on the relation between attitude and television fare because one can reasonably assume that a violent environment leads a person to judge television violence and aggressive film sequences as real and therefore makes him more liable to be influenced by the rationality of the aggressive behavior models on television.

Finally, one can postulate that in an imagined hierarchy of concreteness, television plays a less important part in influencing reinforcement attitudes than do actual daily experiences with aggression, eg. observing actual aggression, being victim of aggression, or acting aggressively on self.

Monroe M. Lefkowitz (New York State Department of Mental Hygiene Abstracts) Violent Television Reference and Depression

Many studies have reported a relationship between a diet of violent television viewing and aggressive behavior in young male children. Moreover, the data strongly indicate that the relationship is causal. Violent television engenders aggressive behavior. To this writer's knowledge, no data are extant concerning the possible relationship between violent television and other kinds of psychopathology. Consequently, the present study examined this relationship in two groups of subjects for which measurements on television violence and psychopathology were obtained. In the first group, data were gathered on television program preferences from 211 male and 216 female subjects whose modal age was 19 years. In addition, the Minnesota Multiphasic Personality Inventory (MMPI) was administered to all subjects. A statistically significant relationship was found between violence ratings of program preferences and the depression scale of the MMPI but only for females. The data also suggested that self-esteem was lower for the females who preferred violent television. These empirical findings prompted collection of data from a second group comprised of 585 children — 334 females and 251 males — whose modal age was 10.4 years. Television viewing preferences and self-ratings of depression and self-esteem were obtained from each child. Based on the prior findings for young adults, it was hypothesized that a preference for violent television would be related to depression in this sample of children. To strengthen the test of this hypothesis, a multimethod approach to the assessment of television violence and depression was used. Essentially, the earlier findings on adults were repeated for children. A statistically significant relationship between television violence and depression across both methods was found for females. Self-esteem was also significantly lower for those females preferring programs containing television violence. The results for males, however, were equivocal. Theoretical considerations to account for the findings of this study are presented.

HUMAN AGGRESSION C

Chair: Richard J. Borden, Purdue University, West Lafayette, Indiana

Ann M. Frodi and Michael E. Lamb (University of North Iowa, Cedar Falls)

Parents' Responses to Infants at Risk for Child Abuse

Demographic evidence suggests that premature infants are three times more at risk for child abuse than any other category. In one study by the present authors, it was found that a crying infant elicited significant autonomic arousal and fear.

ings of an anger and aversion particularly when the infant was labeled as premature whereas a smiling infant elicited pleasant emotions and negligible physiologic changes. In a replication and extension of this study an attempt was made to assess independently the effects of the auditory and visual characteristics of "normal" and premature crying infants on parents' autonomic responses and self-reported emotions. Four six minute videotapes were prepared which recorded 1) a normal infant with its normal cry, 2) normal infant - premature cry, 3) premature infant - premature cry, and 4) premature infant - normal cry. Thirty-two parent couples ($N = 64$) were randomly assigned to these four conditions. Heart rate (HR), skin conductance (SC) and blood pressure (BP) were monitored while the parents viewed the videotape. Thereafter self-report measures were administered. Few sex differences were found on either physiologic or emotional indices. The infant cry triggered significant HR, BP, and SC increases in mothers and fathers as well as negative emotions indicating anger or aversion. More importantly, these responses were significantly stronger to the premature cry than to the normal infant's cry. Aversive reactions and autonomic arousal were particularly pronounced in those parents exposed to both the auditory and visual cues of the premature infant. Incorporated into Berkowitz's model of impulsive aggressive behavior, the results suggest that specific physical and behavioral characteristics of premature infants might well contribute to rendering these infants at risk for child abuse.

Michael T. Hynan (University of Wisconsin-Milwaukee)

Shock Delivery in Human Aggression Experiments: Aggression or Button Pushing?

The construct validity of shock delivery as an indicant of aggression was investigated in a new paradigm of human aggression. After completing the MMPI (scored on 74 scales) and Blackburn's scales of hostility and aggression, 140 college students engaged in a competitive game with a research assistant (identified as such). The subject and the assistant were seated at opposite ends of a table facing nearly identical equipment panels. Each game was a race to determine which competitor would be first to score 300 points on a scoreboard by repeatedly pressing a telegraph key. In addition, both competitors had the option of blocking the progress of the other for five seconds by pressing a second lever on their respective panels. Also, the subject had the option of delivering a brief shock to the assistant's hand by pressing a button on the panel. In one condition (noninstrumental) a shock response served only to deliver shock. In a second condition (instrumental) the shock response also terminated a block delivered by the assistant. Assistants were actually shocked. The 26 personality scales were factor analyzed into three factors: I) anxiety vs ego strength, II) repressiveness vs expressiveness (aggression) and III) degree of psychopathology. Multiple regression analyses indicated that

factor scores from the three factors did not predict use of shock in the instrumental condition. In the noninstrumental condition the three factors did predict shocking factor II accounting for 18% of the total variance in shocking. The construct validity of shock delivery as an indicator of aggression appears to be situation-dependent.

Jacquelyn Gaebelin and Kenneth Gruber (University of North Carolina at Greensboro)

Effects of Target Variables on Third Party Instigated Aggression

This presentation reports the results of a series of studies that have examined the long term consequences for a target of aggression in the third party instigated aggression paradigm.

The first findings noted suggest that a subject's role as either aggressor (who directly attacks) or instigator (who instructs another to attack) affects the amount of aggression directed toward the target. In general nonprovocative victims are the targets of more aggression when a subject is an instigator rather than a direct aggressor.

The second general set of findings suggest that subjects tend to be more influenced by the current behavior of their targets than by past experience. In a number of studies a two phase procedure examined the aggression directed toward the target in phase 2 as a function of events which occurred in phase 1. Generally subjects tend to direct more aggression toward a provocative than a nonprovocative target when the target is the same as in phase 1 but if the target is a different person both the target's provocativeness and subjects' past experience with aggression predict subsequent aggression.

This series of studies provides evidence against the frustration aggression hypothesis and questions the utility of the displacement-of aggression construct. A social learning perspective which emphasizes the interaction of past and current variables best explains the data collected to date. Specifically, the clearer the present situational demands for aggression, the less predictive are past aggressiveness, experience, the more ambiguous the current situation, the more likely past experience of responding aggressively predicts continued aggression.

Christina J. Johns (Michigan Department of Corrections, Lansing)

Female Partners and Male Police

Sixteen male State Police Troopers with either a male or a female partner responded to a training film designed to provoke impulsive aggression. Troopers and partners fired blank loads directly at a movie screen when they felt it would have been appropriate to do so had the situations depicted in the movie been occurring in real life. The hypothesis that female presence would affect shooting

responses of male troopers was confirmed. Troopers with female partners fired more often and with fewer nonshooting errors than did troopers with male partners. The results are discussed in terms of three models of aggressive behavior and the practical applications of the findings.

Vladimir J. Konecni (University of California, San Diego, La Jolla)

Relationship Between Aggression and Experimentally Induced Negative Emotional States (Anger, Fear, Disappointment)

Recent studies have shown that an opportunity to hurt physically an insulting person tends to reduce the amount of subsequent aggression directed by angered people against the annoyer (the cathartic effect). This finding has been interpreted in the context of a more general model of interpersonal aggression which proposed that there is a relationship of *bidirectional causality* of degree of anger and amount of aggression expressed such that a) the higher the degree of anger, the greater the amount of aggression, and b) aggressive actions performed by angry individuals may reduce the degree of anger by virtue of decreasing the level of cardiac arousal (perhaps because the prevailing real life contingencies lead to pairing of aggression with a decrease in arousal that accompanies the removal — through aggression actions — of noxious social stimulation). Such considerations suggest that every instance in which aggression alleviates anger would increase the probability that aggression would occur in future cases of anger induction. The present explanation of the cathartic effect thus has implications for delayed aggressive behavior: its predictions, though not the proposed underlying mechanisms, are similar to those derived from the social learning theory.

To investigate such issues, an experiment was performed to compare the effects of pairing insult-induced anger with a) aggression against the insulting person, b) a nonaggressive activity also known to have arousal and anger-decreasing properties (soothing computer-generated "melodies" at 4.00 bits/tonne) and c) a neutral activity unlikely to lead to a fast decay in arousal and anger. After these manipulations, subjects read light material for 15 minutes to allow a complete arousal decay, and then were again angered (by a different method) in certain conditions and not angered in others. Finally, all subjects had the opportunity to express aggression against the person who had originally insulted them and to expose themselves to the soothing computer-generated melodies ad libitum (these were nonredundant dependent measures). It was found that in comparison with the various control conditions (there was a total of nine conditions with ten subjects in each), subjects whose original anger had been paired with aggression and who were then angered again subsequently aggressed far more than subjects in any other conditions. In contrast, subjects whose original anger had been paired with soothing melodies reacted to the second anger episode

sode by listening to the soothing melodies a great deal (more than in the appropriate control conditions) and aggressing very little (less than in the appropriate control conditions). The predictions were thus fully confirmed.

Two additional experiments explored the effects of pairing aggressive and non-aggressive activities with other negative emotional states (fear, disappointment) on the amount of aggression following a subsequent induction of the same negative state. As predicted, the results differed from those in the case of anger. The theoretical reasons for the differences, as well as the findings from additional related experiments, are discussed.

HUMAN AGGRESSION D

Edward Donnerstein (Iowa State University, Ames)

Effects of Erotic Stimuli on Aggression Against Women

Although the 1970 Presidential Commission on Obscenity and Pornography concluded at the time that there was no evidence of a relationship between exposure to erotic forms of presentations and subsequent aggression, particularly sexual crimes, recent criticisms of these findings have led a number of investigators to reexamine this issue. Specifically, research by a number of individuals has indicated that under appropriate conditions exposure to erotic forms of media presentations can facilitate later aggressive behavior. While this research has been directed at the question of erotic effects on behavior, the issue of whether such media presentations can in some manner be related to increased aggressive attacks against women has been of only recent concern. The present paper discusses a series of recent investigations that have examined the conditions that might facilitate aggression towards women as a function of erotic exposure. On the basis of this research which has investigated both the behavioral and physiologic reactions of male subjects to erotic exposure, it is concluded that certain situations that allow for a reduction in inhibition of aggression can act as to facilitate aggression toward females. The implications of this research for future studies on erotic film content and individual differences in this area are discussed.

Dick Moriarty and Ann McCabe (University of Windsor, Windsor, Ontario)

Studies of Television and Youth Sports: Laboratory/Field Research on the Effects of Prosocial and Antisocial TV Models on Children and Youth

This study reports the results of a research project commissioned by the Ontario Royal Commission on Violence in the Communications Industry. The purpose of this study was to describe the growth and development of TV sports.

athletics aggression and violence and to assess the effects of prosocial and anti social TV sports/athletics on children/youth in Little League baseball minor league baseball and summer hockey The study was conducted in a classical test/retest research design utilizing the SIR/CAR system Audio and written questionnaires were utilized to assess TV viewing habits basic disposition of the children/youth to professional athletics or amateur sport organizational models and attitudes feelings and interactions of children/youth and their parents through a TV diary Binocular rivalry was utilized to test the effects of prosocial antisocial and control instructional TV inputs on the perception of violence and aggression by the children Behavior before and after exposure to prosocial and antisocial or control TV tapes was monitored by TV slides and personal observation Behavior of children/youth while viewing the TV treatment tapes was also monitored The results showed that exposure to antisocial TV models did not significantly change the behavior of the children/youth while exposure to prosocial TV models did appreciably reduce physical and verbal aggression (while marginally increasing symbolic aggression)

Christina J Johns (Michigan Department of Corrections Lansing)

Evolution of Legal Traditions in Mexico

Solutions to social problems in any society are the product of the evolution of that society To understand the solutions one must understand the evolutionary process of the society itself The intent of this article is to provide the reader with a broad understanding of the evolution of legal traditions in Mexico that have shaped legal solutions to social problems The focus is on the legal traditions of two of the major pre-Conquest Indian civilizations the Aztec and the Maya the more important legal issues of the Spanish Conquest and the Spanish legal legacy and the social situation of law and order in Mexico from 1809 to the present There are three themes that are crucial in considering the history of criminal law in Mexico They are 1) a societal orientation toward severity of punishment 2) a tradition of disrespect for law and 3) continued attempts to bring about order through violence The three sections of the article in turn stress these themes

Patricia H Powell (Purdue University West Lafayette Indiana)

Human Animal Aggression An Examination of a Neglected Topic

A survey of existing psychological literature indicates a steadily increasing number of investigations of aggression between humans and of aggression between animals Surprisingly few studies have addressed the issue of human animal aggression In part this neglect is due to the definition of human aggression against animals as predation Nevertheless little information exists regarding either the motivations for human animal aggression or inhibitions against it Ex

tant literature can be classified as 1) psychoanalytic interpretations 2) investigations of animal vs human victims and 3) studies of attitudes toward animals hunting. Studies of attitude provide the most lucrative approach for understanding harm doing behavior. It is suggested that this approach be refined to address specific topics regarding aggression against animals. An understanding of the determinants of human-animal aggression would provide insight into many current social problems. Issues of human-animal aggression and species preservation as well as human treatment of our earthly cohabitators can all be addressed with an understanding of human-animal aggression.

Richard J. Borden (Purdue University, West Lafayette, Indiana)

Towards a Theory of Human-Animal Aggression

Despite a growing interest in the determinants of human-human aggression and animal-animal aggression, very little theoretical attention has been directed toward an understanding of human-animal aggression. In part, this neglect may stem from the traditional and perhaps restrictive definitions of aggression used by many researchers. Nonetheless, human exploitation of animal victims is a widespread and apparently increasing phenomenon. This presentation is designed to examine the theoretical factors that can explain the unique relationships that occur between the human and nonhuman animal species. Particular emphasis is focused on the role of individual, situational, and sociocultural determinants of animal victimization. Further, a theoretical review of the ways in which emotions, values, needs, and habits combine to influence willingness to utilize animals is provided. In addition to providing a framework for guiding hypotheses and research on this topic, this presentation also organizes a conceptual language for a psychological understanding of human-animal relationships.

HUMAN AGGRESSION

Chair: Dagmar Krebs, Institut für Psychologie der Rheinisch-Westfälischen Technischen Hochschule Aachen, Federal Republic of Germany

Carl W. O'Neil (University of Notre Dame, Notre Dame, Indiana)

Some Child Rearing Practices Contributing to Nonaggressive Behavior in a Zapotec Community

Research in the Valley of Oaxaca (largely among Zapotec speakers) discloses the side-by-side existence of relatively aggressive and nonaggressive communities. (Some of these communities have been labeled violent/antiviolent or high/low-

cidal/low-homicidal communities in other research done in Oaxaca) Differences along the dimensions of aggression/nonaggression in these communities are *not* readily explained with reference to differences in cultural traditions (they all more or less share in the same dominant cultural tradition) differences in demographic factors or differences relating to ecologic situations Furthermore there is no clear-cut or explicitly stated religious or philosophic ethic demarcating aggressive and nonaggressive communities

My own research in several field trips over the last ten years leads me to believe that differences in aggressive and nonaggressive social behaviors relate principally to three categories of variables The categories are 1) cognitive orientations toward the relative acceptance or nonacceptance of interpersonal aggression as a common solution to human problems 2) differing emphases on the values placed on the quality of interaction in interpersonal relationships 3) differing practices and expectations in the rearing of children The variable categories referred to in 2 and 3 above are assumed to be supportive of variable category 1 The ethnographic data at least strongly suggest this to be the case in relatively nonaggressive communities While reference is made in this paper to each of these categories of variables the focus is placed on certain empirically relevant child rearing practices which appear to be closely related to customary social behaviors in a nonaggressive Zapotec community well known to the writer Differences in the seriousness of various childhood offenses and how these offenses are handled by parents (based on interviews with fathers and supported with field observations) will be discussed The implications of these practices in the development of a predominantly nonaggressive cognitive orientation will be explored

Jerome R Corsi (University of New Mexico Albuquerque)

Terrorism as a Desperate Game: An Analytic Step Toward Comprehension of Fear Bargaining and Communication in the Terrorist Event

This paper views terrorism from an analytic framework After a definition of terrorism is advanced a typology is presented to identify four different types of terrorist events and characteristics particular to each The typology is generated in a 2 X 2 block utilizing the following dimensions a) terrorist intent ie whether terrorists intend or do not intend to capture persons or property b) target location ie whether the location of the target is known or unknown Most importantly this typology permits distinguishing types of hostage taking from attack terrorism Following this the negotiations involved in hostage taking situations are examined in some detail with emphasis on governmental response options and event outcomes Decision routes are mapped as a method for conceptualizing the tactics involved in bargaining communications

Lawrence Z. Freedman (University of Chicago) and Harold D. Laswell (University, New Haven)

The Dimensions of Terror

ABSTRACT MISSING

ANIMAL AGGRESSION A

Chair: Paul E. Brain, University College of Swansea, Swansea, Great Britain

Douglas Fry (Indiana University, Bloomington)

An Argument Against Group Selection Explanations for Ritualized Aggression

Ritualized aggression that usually does not end with serious bloodshed is common in many animal species, but its evolution is often accounted for in terms of group selection. For instance, Lorenz, Eibl-Eibesfeldt, and others propose that rivals are not killed or seriously injured in within-species aggression because this would endanger the survival of the species. Here, however, it is argued that ritual patterns of interaction, such as ritualized aggression, should be examined in terms of their effects on the fitness of the individuals actually engaged in the behaviors — that is, in terms of updated Darwinian evolutionary theory — rather than group adaptations, which are simply assumed to exist. Maynard Smith's concept of evolutionarily stable strategies for interpreting aggression at the individual level and Hamilton's theory of individual inclusive fitness provide an alternative theoretical framework to group-level explanations. Examples of animal aggression previously interpreted in terms of species advantage are explained in terms of this updated Darwinian approach.

Additionally, it is noted that while there is a growing consensus among evolutionary biologists that selection above the level of the kin group (i.e., group selection) is not the primary force in the evolution of social behaviors, many researchers in other disciplines, being unaware of the problems with group- and species-level explanations, continue to consider the evolution and function of aggressive behavior in terms of group or species benefit. Thus, by making the level of selection issue explicit, it is hoped that a communication gap between disciplines may be partially bridged and that group-level assumptions frequently taken for granted may be critically reexamined.

John F. Knutson and David J. Fordvale (University of Iowa, Iowa City)
 Light Controlled Social Experiences and Aggressive Behavior in the Rat

In a series of recent experiments the influence of colony lighting on both home-cage aggression and shock induced aggression was demonstrated. These studies indicated that subjects raised under a light-dark (LD) light cycle generally display more aggression than subjects raised under 24 hr light (LL) conditions. Furthermore these aggressive behaviors manifested a sinusoidal rhythm in LD groups but not in LL groups. The present experiments were conducted to determine the role of light synchronized social experiences as a factor that mediates these lighting influences on aggression.

The first experiment assessed the role of light synchronized interactions by raising blinded and sighted subjects in cages housing either blinded or sighted cagemates under LD conditions. The results of this study indicate the necessity of a light cycle in determining periodic group rhythms in home-cage and shock induced aggression. Furthermore this experiment provided data that suggested that social interaction is not a potential Zeitgeber for subjects lacking a light cycle Zeitgeber.

The second experiment also raising blinded and sighted subjects with blinded or sighted cagemates maintained subjects under LL conditions. This experiment provided data that suggest that the reported reduction in aggression in LL subjects was due to a constant light produced hyposensitive state and not due to the absence of aggressive experiences. The frequency of home cage and shock induced aggression in blinded rats raised with sighted cagemates was less than that displayed by blinded rats reared with blinded cagemates. On the basis of these data it was concluded that social experience can influence shock induced aggression but the effect is relatively slight.

Richard McCarty (Laboratory of Clinical Science, National Institute of Mental Health, Bethesda, Maryland) and C. H. Southwick (Johns Hopkins University, Baltimore)

Food Deprivation: Its Effects on the Predatory Behavior of Southern Grasshopper Mice (*Onychomys torridus*)

The grasshopper mouse (*Onychomys torridus*) is a predatory and aggressive rodent native to the semiarid scrub deserts of the southwestern United States and northern Mexico. Its natural diet consists mainly of arthropods and small vertebrates. In this study we have evaluated the effects of food deprivation on the predatory behavior of adult male and female grasshopper mice to crickets

and laboratory mice (*Mus musculus*). No sex differences were observed in the predatory behavior of grasshopper mice to living or dead crickets. Subjects were deprived of food for 48 hr spent more time eating and tended to consume more prey than did controls that were provided with free access to food. When food available *ad lib*, 6 of 43 (14%) male and 22 of 45 (49%) female grasshopper mice killed and ate *Mus* opponents within 48 hr of pairing. When deprived of food for 48 hr, 16 of 36 (44%) males and 15 of 19 (79%) females that were killers in the previous experiment killed and ate *Mus* opponents. Thus, food deprivation and type of prey are two factors which influence the predatory behavior of grasshopper mice.

Sami Al Maliki and Paul F. Brain (University College of Swansea, Swansea, Great Britain)

Studies on Different Forms of Aggression in a Laboratory Mouse Strain

A number of authors have proposed schemas to classify types of aggression. These classifications have arisen from the generally accepted conclusion that the concept aggression encompasses a diverse group of activities that are linked simply by the fact that they cause actual or potential harm to another individual. There have already been a number of attempts to contrast different forms of aggression in the rat. The laboratory rat has proved in the past, however, to be an appointing research animal as it has been difficult to induce "spontaneous" aggression in this species. Consequently, a series of studies have been carried out using albino laboratory mice of the Tuck "TO" strain (these animals have already been used in a variety of hormone/aggression correlations). Males of this strain readily show intermale or rank related fighting in standard opponent tests following short periods of isolation or cohabitation with a female. In the first series of studies the effects of simple experimental manipulations on rank related fighting in a standard opponent test were contrasted with the influences on locus killing behavior (a form of predatory aggression?) in the same animals. Variables such as ontogeny, sex, behavioral experience (locust killing or mouse attack), housing condition (isolation or grouping), social rank (dominant or subordinate), performance in a predation test, 36 hr of food deprivation, olfactory cues (sham perfused or rendered anosmic), and gonadal function (sham castrated or castrated) all differentiated between these two forms of aggression. The conclusion reached was that rank related and predatory aggression have very different physiologic bases.

Additional experiments will be described in which rank related and/or locus killing are contrasted with other forms of aggression. These include maternal aggression (seen in lactating female mice), a form of territorial aggression generated by using a series of interconnected cages, and pain induced aggression induced by unavoidable electroshock. Again, differences between the dif-

ferent models were apparent. It is suggested that workers should where possible look at a variety of models before making statements about the effects of treatments on aggression.

ANIMAL AGGRESSION B

Chair: David H. Adams, Wesleyan University, Middletown, Connecticut

Robert J. Shordone (University of California, Los Angeles)

Mescaline Induced Pathological Aggression in Rats: An Explanation of the Phenomenon

The species typical aggressive repertoire of a pair of rats in response to foot shock consists of both rats assuming upright boxing postures and striking each other with their forepaws. Aggressive behavior of which topography and severity significantly exceed this repertoire can be operationally defined as "pathological." When mescaline is administered to a pair of rats in conjunction with foot shock their behavior appears to qualify as pathological since rather than box with an opponent they will engage in vicious biting. This effect has been shown to be highly reliable and relatively unaffected by the size of the testing chamber, fighting experience, shock termination experience with the drug, and age or strain of the animals.

Two studies are reported in which mescaline's effect on both the victim's and the attacker's behavior was investigated. In the first study the topography of the attacker's aggressive behavior was found to be related to specific behaviors elicited by the victim immediately prior to an attack. In the second study the severity or the extent to which the biting attacks produced physical damage to the victim was found to be related to EEG changes in the attacker. These results suggest that mescaline induced pathological aggression in rats is due to changes in both the victim's and the attacker's behavior.

Mahael Potegal, Alan Blau, and Murray Glusman (City University of New York, Flushing)

Suppression of Aggression in Hamsters by Stimulation of the Septal Region

We have recently observed an apparently specific form of aggression inhibition in hamsters produced by stimulation of the septal area. Our subjects were individually housed male golden Syrian hamsters 3-4 months old, selected for aggressiveness and implanted with chronic movable electrodes held with a spring clip skull anchor. These subjects readily attacked nonaggressive target hamsters that were pretreated with an analgesic and muzzled to prevent retaliatory biting.

After evaluation of subject's base line attack rates on targets placed in their home cage the subjects were stimulated in the septal region with 0.1-millisecond biphasic pulses at 100 pps.

At current levels that did not produce any motor automatisms or stereotypic competing responses, septal region stimulation prevented the initiation and expressed the ongoing performance of subjects' attacks on the targets. Stimulation at minimum current levels necessary for aggression inhibition (35–140 μ A) has had no effect on acceptance of sunflower seeds (a highly preferred food for hamsters) in any animals tested to date. In two-thirds of the animals tested to date this stimulation also has not inhibited copulatory behavior with a receptive female. Recordings from the stimulating electrode before and after stimulation have not yielded any indication of seizure activity. Preliminary tests of the reinforcing value of the stimulation in an operant chamber indicated that the stimulation may be moderately aversive. There is some indication that this aversiveness may be minimized when aggression-suppression occurs at lower current levels. These results extend previous reports of septal inhibition of predatory and defensive aggression to include effects on intraspecific aggression.

D. Benton, P. F. Brain and J. F. Goldsmith (University College of Swansea, Swansea, Great Britain)

Involvement of Various Sensory Modalities in Isolation Induced Aggression in Laboratory Mice

Studies of the involvement of olfactory, tactile and visual cues in the development of isolation induced aggression were reported.

The olfactory input of individually housed male mice was decreased by nasal infusions of zinc sulphate, a process found to be associated with a decreased incidence of threat and fighting. The possible role of pheromones was examined by exposing individually housed male mice to the soiled bedding from various groups of mice. Isolated males in the presence of bedding from groups of female displayed significantly less aggression than those in the presence of the bedding from group-housed male mice.

The removal of the mystacial vibrissae increased the tendency for mice experienced in fighting to attack. However, their removal had only a little influence on the development of isolation induced aggression.

Mice able to see other animals through perspex screens were as aggressive as traditionally housed isolates. However, individual mice separated by perforated zinc screens displayed lower levels of fighting.

In most laboratories so-called isolated animals are merely physically separated from conspecifics which they may be able to see, smell and hear. Preliminary experiments were reported in which mice were as far as possible totally isolated. There was a suggestion that total isolation may suppress fighting to a small extent.

It was concluded that one factor influencing isolation induced aggression is physical separation. Olfactory cues also have a significant influence but visual information seems relatively unimportant.

SYMPOSIUM CONSEQUENCES OF SOCIAL ISOLATION UPON PRIMATE BRAIN DEVELOPMENT AND BEHAVIOR

Chair: James W. Prescott, National Institute of Child Health and Human Development, Bethesda, Maryland

Discussants: Robert S. Dow, Good Samaritan Hospital, New York; Ray S. Snider, University of Rochester, Rochester, New York; Al Globus, University of California, Davis

During the past 25 years a wealth of behavioral data have been obtained upon the developmental consequences of rearing infant monkeys in simple cages in which they are deprived of somesthetic and vestibular sensory stimulation that is ordinarily provided by the mother and peers in a normal rearing environment. These studies that were initiated by the Harlows in the mid 1950s have documented the depressive, withdrawn, autistic-like, stereotypical and chronic self-stimulation behaviors in infants reared in isolation and the hyperactivity, hyperreactivity and pathological violence in juvenile and adult monkeys reared in isolation. The studies of Mason and Berkson have implicated vestibular sensory processes in the development of these pathological social and emotional behaviors consequent to isolation rearing. It has been suggested by Prescott that these isolation rearing conditions constitute sensory deprivation of the somesthetic and vestibular modalities which induces neuromorphological, neurochemical and electrophysiological abnormalities in the developing brain. The cerebellum was particularly implicated in the mediation of the isolation rearing syndrome.

The objective of this symposium is to review recent findings of neuropathology resulting from primate isolation rearing, special attention being given to the role of the cerebellum in the mediation and regulation of sensory, social and emotional processes in the infrahuman and human primate.

A. H. Riesen, P. Lehr, B. J. Sonnier and M. G. Struble (University of California, Riverside)

Branching Differences in Stellate Cells Related to Cortical Area and Rearing Environment of Monkeys

Varying conditions of somatosensory stimulation and motor activity were imposed during rearing to investigate possible differences in layer IV stellate cell

branching brain proteins and behavioral development as functions. Samples for determining stellate cell development and for bi determinations were taken from sensory cortical areas (visual soma and II) and from motor (M I - M II) and pre-motor frontal cortex. A stump-tail macaques (*M. arctoides*) born in the laboratory were reared each of four conditions: condition I - a 12-in X 12-in transparent box with grille floor. An attached bottle with protruding nipple and a feeder containing monkey chow gave opportunity for some object manipulation. II - a 48-in X 48-in transparent cube with bottle and hopper, the same as condition I with the addition of sloping ladder, a horizontal swinging trapeze and play objects (small cube, ball, rod). Condition III - immediately adjacent large colony room in which "controls" were in view of all other animals by mothers housed as members of a socially mixed sex group.

Total protein determinations indicated no significant differences in brains of the four groups of animals at 6 months of age. Similar negativity resulted from water-soluble synaptic plasma membrane synaptic cytochrome c and Triton-soluble protein determinations. Samples from cerebellum and corpus callosum were likewise negative.

Behaviorally the animals of conditions I, II, and III showed typical social isolation impairments. Bizarre and stereotyped posturings were observed with the degree of deprivation.

From samples of nonspiny layer IV stellate cells drawn and studied statistically by double-blind procedures, several significant effects have been observed. The visual cortex was not affected. The deprived animals showed significantly increased branching in S I and in M I. The socially deprived but motor-enriched animals of condition III (which were consistently high in activity on the ladders, trapeze, etc.) showed a significantly greater degree of branching in S I, S II, and M I than did all other groups, including the mother-reared controls.

William T. Greenough, Mary Kay Floeter, Gene P. Sackett, *Martin J. Cherry, Cheryl Kraff (University of Illinois at Urbana-Champaign) and *Unne, Washington State.

Experience and Macaque Monkey Brain Development: Relationship to Isolation Syndrome

It has been proposed that the behavioral primate isolation syndrome involves retarded or abnormal maturation of somatosensory cerebellar development and possibly abnormalities in other sensory-motor regions. We have examined the cerebellar flocculus, nodulus, uvula, and vermis in monkeys for signs of abnormal development with quantitative

Golgi cox stained and cresyl violet stained tissue. *Macaca fascicularis* infants were reared for six months from the first week of life in one of three environments: total social isolation (I) in a sound attenuating chamber that prevented visual contact with other animals; restricted social contact (S) in which monkeys housed individually in adjacent cages were paired for four hours per day; or a colony environment (C) containing adult, juvenile, and infant monkeys in a large cage with various play objects. Systematic individual and social behavior measures were made two to four times per week during rearing of groups S and I and social behavior of all groups was studied between 6 and 8 months of age. At 8 months the brain was prepared for anatomic examination. Behavioral analyses showed isolation syndrome characteristics (stereotyped behaviors, abnormal postures, social incompetence, etc.) present at high levels in most I monkeys and infrequent in S and C monkeys. Anatomic analyses showed significantly greater Purkinje cell spiny branchlet size in C monkeys and no differences between S and I groups in paraflocculus and nodulus. There were no differences in granule cell dendritic branching. In the uvula and nodulus, Purkinje cell body size was greater in group C relative to S and I. Further analyses of cerebellar and forebrain regions and comparison with behavioral measures within subjects are in progress.

A. J. Berman (Brooklyn Jewish Medical Center, Brooklyn, New York)

Effects of Cerebellar Decortication Upon Violent and Stereotypical Behaviors in Isolation Reared Monkeys. Film Studies

ABSTRACT MISSING

Robert G. Heath (Tulane University School of Medicine, New Orleans)

Brain Mechanisms in Violent Aggressive Behavior: Rationale for and Results of Treatment by Cerebellar Stimulation

This paper presents a demonstration with reporting depth electrode patients of correlations between deep brain activity and violent aggressive behavior and a demonstration on the basis of anatomic data that there are direct connections between the sites where brain activity correlates with violence and sensory relay and nuclei containing cell reservoirs for chemical transmitters, an interrelated system that is an important component of the neural network for emotional expression.

Experimentation with unit recordings in animals also demonstrates functional relationships within this system, particularly as to the effects of cerebellar stimulation.

Results obtained by application of cerebellar stimulation to violent patients are also reported.

Bernard Saltzberg (Texas Research Institute for Mental Sciences Houston)
Noninvasive Methods for the Detection of Abnormal Deep-Brain Electrical Activity

Intermittent deep-brain electrical spiking activity has been implicated in certain brain and behavioral disorders such as epilepsy and uncontrolled violent aggressive behavior. This paper reports on the development of methods for detecting intermittent complex ELG patterns that are time locked to these abnormal deep brain electrical spiking events.

Studies in monkeys with deep brain implants have demonstrated that the times of occurrence of particular patterns of scalp ELG activity are highly correlated with the times of occurrence of deep brain electrical spikes. In separate studies conducted by R. G. Heath and A. J. Berman such spiking activity proved to be characteristic of monkeys that were raised in isolation—a condition that produced highly aggressive and violent behavior in these nonhuman primates. In view of the results of such invasive studies in monkeys, the approach to the detection problem for noninvasive human studies is based on the postulate that deep brain electrical spiking is reflected in the EEG as a sequence of complex transient patterns that are time locked to depth spikes. The individual transient patterns to be detected may differ in amplitude and interval separation but are assumed to be similar in wave shape.

Examples of digital filtering approaches as well as spectral deconvolution approaches are presented as a basis for detecting transient patterns in the EEG from which deep-brain pathology can be inferred. The particular detection approach selected will depend upon the amount of a priori information available on the times of occurrence of the patterns to be detected as well as on the background EEG activity in which these patterns are embedded. The mathematical model upon which the detection methods are based is discussed in the context of testing hypotheses concerning the presence of deep-brain electrical spiking in the scalp EEG.

SYMPOSIUM TELEVISION AGGRESSION AND CHILD BEHAVIOR
KEY DEVELOPMENTAL AND MENTAL HEALTH ISSUES

Chair: George V. Coelho, National Institute of Mental Health, Rockville, Maryland

Discussant: David Pearl, National Institute of Mental Health, Rockville, Maryland

This symposium brings together leading educators, developmental psychologists, and other social scientists to examine new research and policy issues regarding

in the role of television in the lives of children and especially its impact on their behavior personality and general psychosocial development

The moderator presented an overview of NIMH continuing concerns and research investments since the Surgeon General's Study. Each participant then presented information and perspectives on TV viewing contexts and patterns by reviewing assessing and synthesizing the relevant body of TV research about children in adolescence in their respective areas of concern. Special attention will be paid to ecological factors such as family environment peer group setting and interaction situation. In addition personality cognitive and age/developmental factors in prosocial as well as antisocial aggressive behavior in children who are exposed to different TV programs in different cultural and institutional settings were discussed. As far as possible each participant also focused on results that aid in our understanding of mediating processes and mitigating variables related to viewing habits and preferences of preschool children elementary school children and adolescents through age 18.

Concluding commentary and general discussion was planned so as to place emphasis on new directions in research strategy theory and methodology measurement of learning variables etc and on emerging public concerns in education and broadcasting designed for children.

Tannis MacBeth Williams (University of British Columbia Vancouver)

Differential Impacts of TV on Children: A Natural Experiment in Communities With and Without TV

A longitudinal study of the impact of the inception of television was conducted in three Canadian communities. This research was carried out by several faculty members and graduate students in the Department of Psychology at the University of British Columbia under the direction of Tannis MacBeth Williams.

The focus of the project was on a town given the pseudonym Notel which first obtained television reception (one channel the Canadian-government-owned CBC) in November 1973. Two other towns were chosen for comparison: Unitel and Multitel. All three towns were studied just before Notel received television reception and again two years later. During both phases of the research Unitel had CBC reception and Multitel received CBC and the three major US networks (ABC CBS NBC).

The project included assessments of the impact of television on children's aggressive behavior reading skills associative fluency (creativity) block design and vocabulary scores sex role perceptions and attitudes and participation in community activities. Participation in community activities by adults and problem-solving skills and environmental perceptions of adults were also examined.

The emphasis of the paper presented in this symposium is on the findings concerning the impact of television on children's aggressive behavior. This research was done by L.A. Joy, M.M. Kimball and M.L. Zabrack. Their work included observation of verbal and physical incidents of aggression during free play on the school playgrounds. Five male and five female children in each of the three towns in each of grades 1, 2, 4 and 5 were observed before Notel got television and in each of grades 1, 2, 3 and 4 two years later. Children observed during the first phase of the study were observed again in the second phase, if available. Each child was observed by two trained observers during 21 one-minute intervals over a period of 7-10 days. Reliability was greater than 0.8 in both phases of the study. In addition, teacher ratings and peer ratings of aggressive behavior were obtained for all children in the grades included in the observational study.

The longitudinal study of the 44 children observed both before and after Notel children got television revealed significant increases in both verbal and physical aggression for Notel, but not the other two towns. Before Notel had television reception, there were no town differences in physical aggression. Multitel children were more verbally aggressive than Unitel children. Notel and Unitel children did not differ in verbal aggression. Two years after their town received television, the same Notel children were significantly higher in both verbal and physical aggression than their peers in the other two towns. Boys were more physically aggressive than girls.

3. The cross sectional study of 240 children in the three towns during the two phases of the study revealed that children in Notel were physically more aggressive than their Unitel peers, but not different from Multitel children. On the average, children were more physically aggressive during the second phase of the study and males were more aggressive than females. In verbal aggression during the first phase, Multitel children were higher than children in the other two towns and the latter did not differ significantly. Only Notel children increased significantly in verbal aggression between the first and the second phase of the study. In the second phase, Notel children were more verbally aggressive than children in Multitel, who were in turn more aggressive than children in Unitel. No age differences in aggression were found in the cross sectional analyses. This suggests that differences between the first and second phases obtained in the longitudinal study were not due to developmental change.

In both phases of the study, the teacher and peer ratings were intercorrelated and were also correlated with the observational measures of aggression. Internal validity to those observations.

The findings were discussed in terms of the general role played by television in children's socialization and in terms of the theoretical models concerning the impact of television on the acquisition and performance of aggressive behavior.

Eli A. Rubinstein (State University of New York, Stony Brook)

Involuntary Subliminal TV Intoxication: Some Clinical Issues

Research on the effects of TV violence on the behavior of young viewers has primarily concentrated on normal populations. Very little research has been published on such effects with special populations such as children institutionalized for disturbed behavior. The pertinence of the latter area of research was highlighted by a recent legal effort to defend an adolescent boy in Florida — who was acknowledged to have murdered an elderly woman — on the premise that he suffered temporary insanity due to involuntary subliminal television intoxication. The defense was not upheld because there is no scientific evidence to support such a premise.

This paper describes initial efforts to explore television viewing of institutionalized disturbed children and adults. Findings suggest that television viewing has differential effects on different subgroups of patients. A field study to explore this question further will be described. The implications for utilizing recreational television viewing as a therapeutic tool will be discussed. Furthermore, it will be argued that a study of the effects of television viewing with this population of institutionalized children will provide information relevant to an examination of the role of television in other institutional settings (e.g., homes for the aged, prisons, detention centers).

Albert R. Hollnbeck (National Institute of Mental Health, Bethesda, Maryland)
and Elizabeth J. Susman (Pennsylvania State University, University Park)

Television and Violence: Methodological Issues for Future Research

Current evidence relating the viewing of media violence to the performance of violent acts is stronger than perhaps evidence in any other area of psychology. Generally, the results of investigations support the notion that a wide range of children of all ages, social class backgrounds, and gender perform aggressive acts after viewing violence on television. Furthermore, children who tend to be more aggressive initially are stimulated to higher levels of aggression after viewing televised violence. There are methodological considerations, however, that limit the usefulness of this information for understanding the behavior of children exposed to media violence in the natural context of the home. The purpose of this paper is to identify several of these limitations and to suggest a framework within which future research can be directed toward overcoming those limitations.

A majority of past research on the effects of media violence on children has employed a short-term cross-sectional approach measuring children's behavior in laboratory settings or in group homes for children. The primacy of this approach over others makes the available information regarding the effects of media violence on children deficient in at least two important ways. First, avail-

able evidence is biased against the usual home viewing situation. Media presentations of violence in a research context are presented to children in the unnatural context of the laboratory rather than the setting where most children are exposed to televised and real violence — the home. Second, the effects of age and cohort, the typical marker variables for change, are confounded with time of measurement in the cross sectional design. Changes in the effect of exposure to media violence across ages may be documented using cross sectional designs, but those changes are impossible to interpret from cross sectional designs alone. In sum, research to date has focused on a single exposure or a series of brief exposures to television in a nontypical viewing environment. Thus, the context and the content of the natural viewing environment and how that influences behavior during the impressionable childhood years are gaps in our understanding of the effects of media violence on childhood socialization.

Current trends in developmental psychology indicate that the direction of future research will focus on these two neglected areas. One trend is toward a more ecological perspective which includes the child's home. This viewpoint considers the home environment as a naturalistic laboratory for experimentation. While observing behavior in its natural context, we also must attempt to manipulate the environment in order to understand the basis for the observed behavior. Television is certainly a manipulatable variable. A second trend of developmental psychology is toward a life span perspective of developmental change. This approach provides a methodological framework in which to examine long term effects of media exposure to violence. It would appear that major gaps in our knowledge of the effects of media exposure to violence during childhood years can be corrected through studies which incorporate either or both of these perspectives.

SYMPOSIUM: THE BIOLOGY OF AGGRESSION

Chair: John Paul Scott, Bowling Green State University, Bowling Green, Ohio

Discussant: Paul MacLean, National Institute of Mental Health, Bethesda, Maryland

Robert J. Blanchard, D. Caroline Blanchard, and Lorry K. Takahashi (University of Hawaii at Manoa, Honolulu)

Pain and Aggression in the Rat

The hypothesis that pain produces aggression was examined by comparison of behaviors in an established rat colony (for dominant colony males and strange intruders) to those seen in reflexive fighting and in a tube test involving tail shock. During reflexive fighting, dominant colony rats switched abruptly from the strict

pattern displayed in the colony to show activities (boxing freezing) typical of colony intruders in either task. Moreover, forelimb movements similar to the "strokes" seen in reflexive fighting could be obtained during foot shock to rats held alone on the grid. Finally, bites to an anesthetized conspecific were potentiated by foot shock or tail shock but only when the snout (rather than other body sites) could be bitten. Such snout bites are typical of colony intruders and not of attacking colony rats.

When male and female rats' behaviors were compared in the tube test, male biting and wounding of the snout of an anesthetized male conspecific was a direct function of the intensity of tail shock; the number of bites declining systematically in the time interval after shock. Female rats' biting of male rats was also dependent on shock but did not produce wounds.

However, when an anesthetized cat was presented in the same situation, females bit and wounded the cat even before shock was given, while the males again bit only in response to shock. These data were interpreted as indicating that male biting of both a conspecific and a predator fits the same defensive biting pattern. In contrast, female biting of a male rat is actively inhibited, while female biting of a predator is neither inhibited nor shock dependent. The latter finding may reflect the adaptive value (protection of the young) of attacking a predator before it actually hurts the female rat.

All of these data suggest that the defensive biting pattern elicited by pain or by the proximity of a predator (when the subject is restrained) differs in every detail from the activities typical of a dominant colony rat attacking colony intruders. There is excellent agreement, however, between pain-elicited behaviors and the defensive activities of colony intruders, suggesting that pain produces not aggressive but defensive behavior.

Klaus A. Miczek (Carnegie Mellon University, Pittsburgh)

Drug Effects on Attack, Threat, Defense, and Submission in Laboratory Rats

Sequences of agonistic interactions between two rats were generated by three procedures: 1) omission of food reinforcement in a runway situation; 2) intrusion by a rat into the homecage of selected, isolated and food-deprived rats; and 3) intrusion by a rat into a colony of rats with an alpha animal. The topography of fighting was similar in all three situations (16-mm film) and included all major components of attack, threat, defense, submission, and flight. Frequency, duration, and temporal pattern of salient behavioral elements constituting fighting behavior were measured by two observers actuating keyboards. Drugs were administered to either dominant or subordinate opponents via IP or IM route, 14–45 minutes before test. Administration of low doses of d-amphetamine (0.063–0.1 mg/kg), chlordiazepoxide (5 mg/kg), alcohol (0.5 g/ml/kg), and L-DOPA (10 mg/kg) increased the frequency of attacks and threats toward intruder rats. Intermediate doses of these drugs suppressed attack and threat behavior without affecting lo-

comotor activity. In contrast to these biphasic drug effects, α -tetrahydrocannabinol (THC 0.125–4 mg/kg) and cocaine (0.5–32 mg/kg) failed to enhance behavior over a wide dose range. THC selectively suppressed attacks at very low doses. However, when amphetamine, L-DOPA, alcohol, or THC were administered to the intruder or subordinate animal, considerably higher doses were necessary to alter the reaction of defense, submission, and flight than those affecting the attack pattern. Nondrugged resident dominant rats altered their behavior as a function of the opponent's drug state; amphetamine, L-DOPA, alcohol, and treated intruder rats were attacked and injured more often than placebo-treated rats. Pharmacologic manipulations differentiate between an attack threat pattern and a defensive, submissive pattern.

David B. Adams (Wesleyan University, Middletown, Connecticut)

Brain Mechanisms of Offense, Defense, and Submission

A progress report is offered on a long-term project to map out the neural circuitry underlying aggressive behavior in mammals. The project began with single neuron recording in the midbrain central gray and ventromedial hypothalamus of the cat during affective defense behavior. It was developed further by ethological and lesion studies on intraspecific aggressive behavior of muroid rodents, especially the laboratory rat. The present report attempts to synthesize these two approaches and offers a working model of neural circuitry for both cat and muroid rodents.

Ethological studies on muroid rodents have suggested that aggressive behavior may be organized around three motivational mechanisms: offense, defense (equivalent of affective defense in the cat), and submission. These motivational mechanisms, it is hypothesized, consist of homogeneous pools of neurons that are activated by motivating stimuli and/or hormones. Each motivational mechanism, when active, then activates its own peculiar set of motor patterning mechanisms, which produce measurable or observable motor patterns in the presence of appropriate releasing and directing stimuli.

The motivational mechanism of offense in muroid rodents has not been localized. It may be activated by motivating stimuli which include unfamiliar conspecific odors (processed perhaps in the basolateral amygdala) and—in males only—by testosterone-dependent pheromones (processed perhaps by the olfactory tubercle). It is also activated during competitive fighting, which may be mediated by the amygdala. The motor patterning mechanism of offense includes approach, bite and kick attack (directed to the flank of the opponent), offensive sideways posture, offensive upright posture, and various threat patterns.

The motivational mechanism of defense is apparently located in the midbrain central gray of both cats and muroid rodents. It may be activated by many types of motivating stimuli, which include pain (via the paleospinothalamic pathway), sudden auditory stimuli (via the lateral lemniscus but not requiring the inferior

- colliculus) and large moving visual stimuli (perhaps via the pretectum) Defense may also be activated via forebrain circuits that traverse the perifornical hypothalamus but the forebrain is not necessary for defense behavior The motor patterning mechanism activated by defense in muroid rodents includes freezing flight defensive upright posture threat patterns and — characteristically — lunge and bite attack directed at the face of the opponent Defense is rarely observed in laboratory animals but is commonly seen in wild animals during maternal nest defense and in laboratory animals following olfactory or forebrain lesions

The motivational mechanism of submission is apparently located in the mid brain central gray It may be activated by the same motivating stimuli as those of defense Its motor patterns in muroid rodents include freezing flight defensive upright posture full submissive posture threat patterns ultrasound but *not* lunge and bite attack Submission is often observed in laboratory animals that are attacked

- The forebrain it is suggested switches an animal from defense to submission in the presence of familiar conspecific (conspecific laboratory technician etc) stimuli More specifically it is suggested that the neural circuitry of the ventromedial hypothalamus is a logical and gate switch that is activated by the confluence of amygdala and septal inputs (representing familiar conspecific stimuli) and mid brain central gray input (representing defense inputs) and that it inhibits the defense motivational mechanism and facilitates the submission motivational mechanism

J M Koolhaas (State University of Groningen The Netherlands)

The Hypothalamus and Types of Aggressive Behavior in the Rat

Aggressive behavior of male rats can be observed in a variety of situations and seems to serve a variety of goals The experiments presented indicate that different types of aggressive behavior are not only elicited by different external stimuli but are also based on different internal mechanisms

- Electrical stimulation of the lateral hypothalamus (LH) elicits either of two types of aggressive behavior in the presence of a male conspecific One type closely resembles behavior performed in a territorial situation characterized by fighting and several threatening postures and a strong orientation of the behavior towards the opponent In the second type these threatening postures are rare the stimulated animal just wanders about fighting only when it happens to meet the opponent This behavior may be described as reactive fighting The data suggest a slightly different electrode localization for these two types of aggressive behavior

Lesions in the ventromedial hypothalamus (VMH) can facilitate either of these types of intraspecific aggressive behavior depending on the exact location of the lesion Posterior VMH lesions facilitate territorial aggressive behavior whereas anterior VMH lesions increase the tendency to perform reactive fighting

Both the stimulation and the lesion procedures described here appear to enhance the occurrence of aggressive behavior specifically. It is concluded that at the level of the VMH and of the LH neural mechanisms seem to exist that underlie either defensive or offensive aspects of aggressive behavior.

Alan I. Leshner and Kerry E. Roche (Bucknell University, Lewisburg, Pennsylvania)

ACTH and Vasopressin Treatments Immediately After a Defeat Increase Future Submissiveness

Earlier studies have suggested that the hormonal responses to defeat can serve behaviorally adaptive functions by feeding back and modifying either *current* or future agonistic responses. These earlier studies have used the technique of preventing hormonal responses and observing behavioral changes subsequent to defeat. We report here the results of two studies using the opposite approach. These studies examined the effects on future submissiveness of augmenting the usual hormonal responses to defeat by exogenous hormone treatments.

Mice were subjected to an initial defeat by an unfamiliar conspecific and immediately with either ACTH, lysine vasopressin, or a saline placebo. They then were tested for submissiveness at either 24 hours, 48 hours, or seven days after initial agonistic experience and hormone treatment. Postdefeat treatment with either ACTH or vasopressin increased future submissiveness relative to control, although the time courses of the effects of the two hormones were different. Postdefeat treatment with ACTH increased submissiveness when measured at 24 and 48 hours after the initial experience but not when measured at seven days. On the other hand, postdefeat treatment with vasopressin still affected submissiveness when measured at seven days. These results are interpreted as supporting the hypothesis that the acute hormonal responses to defeat can feed back and modify future agonistic, in this case submissive, responses.

SYMPOSIUM: FACES OF ANTIVIOLENCE

Chair: John Paddock, Institute of Oaxaca, Oaxaca, Mexico

Several villages and towns in one arm of the Valley of Oaxaca, in southern Mexico, have what may be called unnaturally low homicide rates that is, their rates are only a fraction of those prevailing in neighboring and outwardly similar communities in the valley as a whole and in the state. These low homicide rates appear to reflect a general attitude of repudiation of interpersonal violence and the phenomenon is termed antiviolence.

At the 1974 meeting of the International Society for Research on Aggression the idea of antiviolenence was presented and some first tentative indications from a pilot study were sketched out. Now the researchers concerned are able to flesh out several aspects of the picture. In addition the possibility of developing a theory of antiviolenence is suggested for while it is not common anywhere it appears in slightly variant forms in a number of widely scattered parts of the world and may therefore be a pan human development whose clarification in the present study may lead to future generalizations.

John Paddock (Institute of Oaxaca Studies Oaxaca Mexico)

Introduction The Study as Science

Anthropologists in ISRA are a small minority hence some explanation of our methods may be helpful.

First in the matter of the place of anthropology within science some including a few anthropologists think anthropology belongs in the humanities not the sciences. This may be especially true for psychological social and cultural anthropology in which areas most of our work occurs.

Next in regard to science and violence the question arises Is the scientific study of violence possible? Looking at several of the most distinguished post 1967 books on violence we seem to see a trend toward increasingly scientific analyses.

Finally as to anthropology and antiviolenence one might ask why we resort so little to such protective devices as questionnaires and tests and so much to observation of antiviolenent human beings as they go about their usual activities even though this means we are subject to constant accusations of being unscientific. The argument oversimplified is this. No amount of laboratory observation and experiment plus statistical manipulation can produce the information that one obtains by watching the human animal behave in its own habitat the approaches are complementary.

Rose Wax Hauer (Institute of Oaxaca Studies Oaxaca Mexico)

A Psychodynamic Face Learning to Be Violent Vs Learning to Be Antiviolenent

Sentence completion tests were given to all fifth and sixth grade children in 10 Valley of Oaxaca communities which differ in their frequency of violence (or degree of antiviolenence) but share a Zapotec Indian culture. Responses from one violence prone town were highly revealing of underlying dynamics. Those relating to the present theme are analyzed and compared with responses from an antiviolenent town of similar size.

The tests show marked differences in images of self and of adults in male female relations in intensity of emotion expressed and in attitudes toward authority.

Contrasts in child rearing are plainly reflected. The violence prone town shows conditional love parental inconsistency and arbitrariness and greater use of pun

ishment. The contrasting responses serve to illuminate the psychodynamics of machismo. Additionally, they show that the lesser degree of machismo of the antiviolen town appears to be related to greater possibility for ego development in Jane Loevinger's terms.

Responses show that in the violence prone town there is an alternate pattern that places a high value on individual achievement. In the antiviolen town by contrast, responses indicate that the good of the group and conformity to its demands are more highly valued. Respect for authority there involves more cooperation and reciprocity.

Margaret L. Sumner (Institute of Oaxaca Studies, Oaxaca, Mexico)

A Social Fact: Social Structure and Control in an Antiviolen Village

As the other papers imply, one necessary condition for maintenance of an antiviolen community as such is the development of persons characterized by conceptions and feelings and habits that lead to antiviolen behavior. Another necessary condition is a type or types of social structure and social control that induce and reward such behavior.

Traits characteristic of antiviolen San Francisco appear also in San Juan, a village where I have done research for three years. Here I indicate some ways in which a positive self image, a low intensity of affect and little preoccupation with feelings, a reciprocal concept of authority, and a low development of male anxiety and need to prove one's maleness enter into role definition and performance in San Juan polity, family, and child development.

Since male violence is considered far more threatening than female violence, emphasis falls on the roles of men as citizens, husbands, and fathers. The personality resources listed here maintain and are fostered by the key civic values of village solidarity and integrity, and individuals are constrained to conformity with group norms by sensitivity to public sentiment through seeking the desirable esteem and cooperation of others while maneuvering to avoid their much feared ill will.

E. Paul Morrissy (St. Thomas University, Fredericton, New Brunswick, Canada)

A Governmental Face: Formal and Real Mechanisms of Conflict Resolution in an Antiviolen Town

San Francisco, a peasant town of around 5,000 inhabitants, is characterized by (among other things) a strikingly low homicide rate. A study of town government suggests a model of interlocking domains in social control, coming to ether in a system notable for diffusion and low intensity of human interrelationships. Thus, whereas the domains and their sociopolitical functions are similar in San Francisco and in its violence prone neighbors, in San Francisco there are mechanisms for maintaining a low level of intensity (in Rodene Gorney's sense of the term) and this makes possible maintenance of a nearly homicide free town.

- Management of conflict was observed typical patterns are noted and an unusual problem is followed through in detail

While comparisons with violence prone towns are still inadequate some proposals are advanced regarding peculiarities of this antiviolen town in the areas of acquiring influential roles the exercise of power access to the political process manipulation of authority and persuading individuals to follow the community's rules when this implies sacrifice of personal interest

Carl W O'Neill (University of Notre Dame Notre Dame Indiana)

An Individual Face Antiviolen Behavior and Some of Its Hypothetical Personality Correlates A Paradox Within an Enigma

After comparison of ecologic demographic and familiar social and cultural factors has failed to explain the striking differences in levels of interpersonal violence among Valley of Oaxaca communities one looks to formal religious and ethical core values but these too appear to differ little if at all (except of course the attitude toward violence itself)

What independent variables then account best for the strong differences of behavior in the area of interpersonal violence? Child rearing practices and childhood experiences appear to be distinctive in the antiviolen communities and one may predict the occurrence of some personality correlates of these factors

Observations over a number of years in one antiviolen community analyzed in the context of social learning theory suggest that two of these hypothetical correlates are strong needs for social compliance which I call social dependency and deep seated dispositions toward hostility

Antiviolen behavior among people who readily generate hostile impulses is paradoxical enough but this paradox exists within an enigma the occurrence of antiviolen communities in circumstances that seem to favor the opposite Nevertheless the paradox can be transformed into an explanation Hostile impulses may generate not only violence but antiviolen as well

Wayne W Kappel (Temple University Philadelphia)

A Biological Face Violent Deaths in an Antiviolen Town a Record of a Century of Life and Death

This anomaly of frequent homicide in an antiviolen community is examined through an analysis of homicides recorded in local civil records

The best predictor of homicide in these records is the degree to which victims or assailants or both are defined as insiders or outsiders in the local structure as community members or not People who are locally defined as outsiders contribute overwhelmingly to homicides both as victims and as assailants

In socializing (or resocializing) outsiders many of whom are migrants strong pressure exists to conform to the values of the local social order and the conditions

Lrica Rosenfeld Susan Maloney L. Rowell Huesmann Leonard D. Eron
Paulette Fischer Vita Musonis and Ann Washington (University of Illinois at
Chicago Circle)

Effect of Fantasy Behaviors and Fantasy Reality Discriminations on the Observational Learning of Aggression

In recent years a body of evidence has emerged that suggests that a child's perception of media violence as fantasy or reality influences the degree to which the child imitates the observed behaviors. Research suggests that there is greater modeling of aggressive behaviors when the behaviors are labeled as real than when labeled as fantasy; that children who can easily distinguish fantasy from reality are less likely to be adversely affected by media violence; and that children who are predisposed to high fantasy are less aggressive. In a 1972 study Eron, Huesmann, Lefkowitz, and Walder also found that girls perceive TV as less realistic than do boys and model aggressive behavior on TV less. However, it remains to be demonstrated whether different styles of fantasy relate differently to aggression and whether a reduction in modeling of aggressive behavior could be engendered by teaching fantasy reality distinctions. The current study was designed to explore these questions.

The subjects were 748 boys and girls from the first and third grades in Oak Park, Illinois, who were participating in a three-year observational study of factors affecting the modeling of aggressive behavior. Among the measures administered to subjects in two 40-minute testing sessions were 1) a peer-nominated measure of aggression, 2) a measure of how realistic subjects thought various TV programs were, 3) a measure of the amount of TV violence watched, and 4) a new 45-item fantasy questionnaire called the Imaginal Processes Inventory for Children (IPI-C). By factor analyzing the nine IPI-C scales, three styles of fantasy emerged which were remarkably similar to the adult factors of daydreaming found by Singer and Antrobus in 1972. The fantasy styles are 1) action-intellectual fantasy, 2) fanciful intense fantasy, and 3) negative aggressive fantasy.

A clear positive relation was again found between viewing TV violence and aggression. Additional evidence suggests that a child's view of the degree of realism of television related positively to aggression (particularly for girls) and may act somewhat to mediate the relation between viewing of TV violence and aggression. It is also apparent that for boys negative aggressive fantasy is predictive of overt aggression, while for girls action fantasy and negative aggressive fantasy are predictive.

Those children identified as viewers of moderate or high amounts of violence in the first wave of the study were selected for the field experiment and then were randomly divided into an experimental and control group of 100 subjects each. A pretest was administered measuring each child's judgment of realism for

specific aggressive behaviors seen on TV. The experimental subjects were then exposed to three training sessions at three week intervals in which they watched a five-minute tape of a TV program and then participated in discussions structured to elicit fantasy behaviors, fantasy reality discriminations, and imaginative play. The control group received a similar three sessions in which no fantasy was elicited. A posttest of the child's assessment of TV realism was given to each child several weeks after the conclusion of the training procedure.

On the whole, the realism training produced disappointing results. At best it seems that the experimental subjects improved their perception of reality slightly while the control subjects' perceptions worsened. Nevertheless, it was true that the training did have some effect, particularly upon those subjects who initially believed TV shows were realistic but had a neutral sex role orientation and did not identify with aggressive TV characters.

It is believed that the procedure was not more successful because the effect of training may have been counteracted by the use of aggressive and action fantasy material in the training procedure. Aggressive and action fantasy, we found in the first part of this study, are positively related to aggression in children.

L. Rowell Huesmann, Paulette Fischer, Leonard M. Eron, Rebecca Mermelstein, Esther Kaplan-Shain, and Sharon Monkawa (University of Illinois at Chicago Circle)

Children's Sex Role Preference, Sex of Television Model, and Imitation of Aggressive Behaviors

An important finding in early field studies of aggression and viewing of television violence was that females were less affected by viewing violence than were males. In a ten year longitudinal study conducted between 1960 and 1970, Eron, Huesman, Lefkowitz, and Walder found a significant positive relation for boys between aggression and television violence viewing but no evidence of such a relation for girls. One possible explanation for this lack of modeling effect in girls was the lack of aggressive female models in the medium at that period of time. Another possible explanation is the differential reinforcement of aggressive behavior due to differential socialization processes for boys and girls.

The current study is an attempt to measure more precisely the effect of sex roles on observational learning of aggressive behaviors. The subjects are 748 boys and girls who constitute that part of the first and third grade population of Oak Park, Illinois, for whom permission could be obtained. The subjects are being tested and interviewed in each of three consecutive years. In each year, a subject's aggressiveness is measured by a peer nomination procedure, and measures are obtained of self-reported viewing of male violence and female violence on television, self-reported similarity to television characters, and sex role preference. The sex role scale allows the subject to select neutral, masculine, or

feminine items so that a subject is not forced into either a masculine or feminine category

Results from the first year of study indicate that viewing of television violence is significantly positively related to aggression in both boys and girls. However, while the relation is getting stronger with age for boys, it is getting weaker with age for girls. Furthermore, sex role preference is clearly related to peer-rated aggression. Peer-rated aggression is significantly positively related to a masculine sex role preference for both boys and girls and significantly negatively related to a neutral sex role preference. However, the sex of the aggression actor on TV did not differentially affect the modeling of aggression by boys and girls.

In general, these results seem most consistent with the socialization hypotheses for explaining differences between boys and girls in the observational learning of aggression. Girls are generally not reinforced for engaging in overt aggressive acts and the relation between viewing of violence and overt aggression decreases as girls become older. The more overtly aggressive girl is one who is lower on feminine and neutral sex role identification, who is higher on masculine identification, and who engages in action-oriented fantasies. On the other hand, as boys become older, they are taught that some aggressive behavior is acceptable. As a result, the relation between viewing of TV violence and aggression becomes clearer as boys become older. The more overtly aggressive boy is one who is higher on masculine sex role orientation and who engages in negative aggression fantasies.

Charles W. Turner and Michael R. Fenn (University of Utah, Salt Lake City)
Instigating Effects of Associated Retrieval Cues and White Noise on Delayed Verbal Aggression

The present research investigated the delayed behavioral impact of verbally aggressive stimuli which were or were not reinstated from memory via associated retrieval cues. A 2×2 between subjects factorial design was employed to manipulate intensity of white noise (soft vs loud) for induced arousal and connotation of the verbal material to be recalled (nonaggressive vs aggressive). Sixty-two male undergraduates participated in three tasks that introduced the experimental manipulations. Subjects first learned 60 paired associates that varied the connotation of the stimuli to be remembered: aggressive vs nonaggressive. The second task introduced a 15-minute nonrehearsal delay. Thereafter, subjects ostensibly interacted with a fellow subject by writing, exchanging, and then evaluating self-descriptions as part of a social learning task. Prior to evaluating their (nonexistent) partners' self-descriptions, subjects were aroused by one of two levels of white noise and given retrieval cues to reinstate either the aggressive or nonaggressive words they had previously learned. The main measure of verbal aggression

ion was derived from the written partner evaluations. The results indicated that subjects given aggression associated retrieval cues and simultaneously exposed to loud white noise were significantly more verbally aggressive ($P < 0.01$) than subjects in the other three experimental conditions. The results support the thesis that the presence of retrieval cues associated with aggressive stimuli may facilitate a delayed aggressive reaction if subjects are also aroused and disinhibited.

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Differential Aggressiveness and Litigiousness Social Support and Social Status Hypotheses

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The Qolla Indians have high rates of involvement in agonistic forms of interaction. In previous reports the author suggested that ecological and physiological factors are causally associated with intracommunity differential participation in aggressive behavior. The present article described tests of hypotheses using other variables to explain this behavioral differentiation. The hypothesis that aggressiveness and participation in litigation are a function of the amount of social support the individual can potentially mobilize is tested. The relationships between indicators of social status (wealth, education, political activities, and ritual participation) on the one hand, and aggressiveness and litigiousness, on the other, also are examined.

Key words: law and conflict, aggressiveness, Qolla, social status, social support, litigiousness, Peru.

INTRODUCTION

Over the years the Qolla have acquired a reputation for aggressiveness and hostility. Anthropologists and other scholars, both foreigners and native Andeans, have repeatedly stressed the salience of this dimension of Qolla character, and there can be little doubt that interpersonal conflict is pervasive in community life [cf. Bolton 1973]. However, two reservations must be registered with respect to Qolla aggressiveness.

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First this one strand does not constitute the whole cloth of Qolla personality. Without necessarily denying the importance of aggression in Qolla social life, numerous investigators, especially those who have studied Aymara speakers in post-revolutionary Bolivia, have pointed out quite correctly that Qolla conduct is not unidimensional. Carter [1968] for example writes of "positive balances which permit Qolla (or Aymara) society to function" and Heath [1969, personal communication] suggests that an "amiable side" to the Qolla exists.

Second, as in all societies, among the Qolla individuals vary in their levels of aggressiveness, litigiousness, and hostility; they do not participate in equal measure in interpersonal strife and agonistic behavior. The oft-heard Qolla remark, "No somos iguales," certainly applies to aggressiveness. Furthermore, the Qolla recognize and verbalize their awareness of this behavioral diversity. They say that some people are abusive (*abusivo*) and other people are humble (*humilde*). The purpose of this paper, then, is to contribute to an understanding of the causes of differentiation in levels of individual aggressiveness and litigiousness within one Qolla community.

The analysis to follow is not the first attack on this problem. In other writings [Bolton 1970, 1973, 1976] it has been argued that part of this behavioral differentiation could be accounted for by biological variations within the Qolla population. More precisely, I tested the hypothesis that there is a relationship between degrees of aggressiveness and differences in the functioning of glucose homeostatic mechanisms. Results supported the hypothesis: aggressive subjects displayed a strong tendency to be moderately hypoglycemic. Nonetheless, when considering the full range of differentiation, hypoglycemia is capable of explaining only part of the variance in aggressiveness and agonistic behavior. What factors are responsible for the remainder of the variance?

Moyer [1971] notes that aggression is not a unitary phenomenon. Rather, there are various kinds of aggression: predatory, fear-induced, irritable, territorial, maternal, and instrumental. Each class of aggression, according to Moyer, has its distinctive physiological basis. Hypoglycemia is one factor in the etiology of irritable aggression. It is likely that other biological variables will be found to account for additional portions of the variance in Qolla aggressiveness: testosterone levels, for example, to mention one possibility.

We were forced to explore the biological basis of Qolla aggressiveness by the seemingly irrational nature of this behavior. Instead of being goal-oriented and calculated to bring economic or social benefits to the aggressor, most acts of aggression that came to our attention appeared to be expressive and spontaneous. But the question must be asked: To what extent is Qolla agonistic behavior instrumental? Instrumental aggression does occur, to be sure — e.g., cases of fighting over land, of utilitarian stealing, and of failing to pay debts. If instrumental aggression is important among the Qolla, then one should expect to find a series of social factors associated with the differentiation in individual aggressiveness and litigiousness.

ress such factors may either lead an individual to be aggressive or enter into his calculations of the likelihood of success of agonistic behavior. There should be positive relationships between the levels of aggressiveness and litigiousness of an individual and the amount of social support which he is capable of mobilizing and an association between socioeconomic status and aggressiveness. These relationships are analyzed below after some essential background information is presented.

THE ETHNOGRAPHIC SETTING

The Qolla inhabit the Lake Titicaca basin in the border region of Peru and Bolivia at an altitude of approximately 3 800 meters and above. Although the Qolla numbering more than one and one half million are divided between Quechua speakers and Aymara speakers, Qolla culture is fairly homogeneous and set off from surrounding Andean cultures by a set of traits which includes such items as the presence of a dispersed settlement pattern and the absence of maize as an important staple crop.

While most Qolla are small scale subsistence farmers at higher altitudes one finds communities of alpaca and llama herders. The research reported in this paper was carried out in the village of Incawatana on the Peruvian shore of Lake Titicaca in the Quechua speaking zone.* The staple crop for the campesinos of Incawatana is potatoes. This item is supplemented with broad beans, peas, barley, oats, quinoa, oca and some minor cultigens produced in small quantities. The limited availability of pastures and totora reed beds keeps animal husbandry at a minimum in this community although each household manages to raise a few animals: cattle, sheep, pigs and guinea pigs principally. Additional income is generated through part time activities such as fishing, craft production and seasonal migration and employment as burden-carriers and construction workers in urban centers of the region and along the Pacific coast.

The basic social unit in Incawatana is the household. The Qolla are monogamous and the preferred domestic group is the nuclear family. A large percentage of households in Incawatana nonetheless contain one or more aggregated individuals — e.g. son-in-law, daughter-in-law, grandchild or an aged parent of one of the spouses. The 1 200 residents of Incawatana form 230 households.

Although descent is reckoned patrilineally [Bolton 1977] for most purposes the bilateral network of kinsmen for all adults in a household provides the basis for significant links to other households. Ritual kinship bonds established through baptism, haircutting and marriage create further links to other households (see below). Peasants in Incawatana own their land, an average of one hectare per household. Inheritance is bilateral and property is divided equally among siblings, male and female.

*The names of villages and persons are pseudonymous for obvious reasons.

Incawatana is a *parcialidad* or free community: no hacienda exists within or adjacent to the community. Almost all land is owned by residents of Incawatana. The village occupies the lowest position in the national governmental system. The authorities within Incawatana are appointed by the various officials in the district capital Qochapata: sometimes upon recommendation by the outside authorities or the assembly of community members. The most prominent authorities in the village, the *tenientes politicos*, are responsible to the district governor for the maintenance of peace and order within their jurisdiction (Bolton and Bolton 1975).

THE DATA

My assistants and I lived and worked in Incawatana for two years (November 1968 to December 1970). During this period we gathered observational material, copied archival records, and conducted both formal and informal interviews. We paid special attention to the topics of interpersonal conflict and aggression, developing a file of more than 800 cases of strife which had been handled by the village or district remedy agents. In the second half of 1969 we carried out a comprehensive census and genealogical investigation, interviewing all but about ten household heads.

In order to concentrate more intensively on a segment of this universe, we chose a sample of 125 adult males. These men, selected randomly within each of the village's seven sectors, were visited and interviewed at least once each month. When physiological data were obtained, for various reasons only 66 men from the original sample were utilized (e.g. some subjects were absent from the village at the time). For the present analysis this reduced sample is employed because we lack information on some variables for the complete sample.

The dependent variables, aggressiveness and litigiousness, have been operationalized as follows. First, three key informants ranked the 66 men in the reduced sample with respect to aggressiveness. Each key informant performed this task twice. The rankings of one informant were not included in the overall ranking since the correlation of his first and second lists was unacceptably low, and neither of his lists correlated satisfactorily with the rankings done by the other key informants. The latter informants, on the other hand, performed better. Their rating-rerating correlations were 0.92 and 0.78, and the average correlation of their four rankings was 0.76, which is satisfactory for this indicator of aggressiveness.

The second variable involves the frequency of participation in conflicts brought to the attention of public remedy agents. Through examination of the cases in the file, we have calculated the extent of conflict participation for each individual in the sample during the ten year period preceding our field work. Complainant or plaintiff (*demandante*) status and defendant (*demandado*) status are examined separately and in combination.

The independent variables social support and social status have been operationalized as follows. Information on the size of an individual's potential social support set (to be defined below) is taken directly from the census and genealogical inquiry. In some instances we have corrected inaccurate self reports with information obtained informally or from the censuses of kinsmen. Unfortunately we have not been able to complete the complex task of verifying self reports on ritual kin sets and we suspect that this information is incomplete especially with respect to the number of times the subject has served as godfather (*padrino*) for the children of others. Yet we have no reason to think that this incompleteness is associated differentially with levels of aggressiveness.

Measurements for three indicators of social status (age, education, and participation in communal rituals and political affairs) have been derived from the census. Wealth has been operationalized in two forms: 1) self reports on ownership of livestock, and 2) intra sector rankings of subjects performed by two key informants. Finally, birth order data are taken from the genealogical inquiry.

AGONISTIC DIVERSITY

Key informants appeared to experience no difficulty in ranking the 66 subjects on their aggressiveness. And when we add the scores obtained by each individual on the four rankings we discover that the informants have utilized almost the entire potential range of differentiation. That is, technically the scores could range from 4 points (highly aggressive) through 264 points (nonaggressive); the actual scores started at 7 points and ended at 263 points. Reputations for aggressiveness then can be seen to vary tremendously.

This differentiation is visible also in the rates of participation in litigation. Table I contains litigation data for 64 subjects for a period of approximately ten years. Only one subject participated in no litigation during this period according to our records, while one individual was a plaintiff or defendant in 21 cases. As plaintiffs the subjects in our sample participated in — indeed initiated — a mean of 3.47 cases (mode = 6, median = 3, and range = 0–10 cases). As defendants the subjects were involved in 3.97 cases on the average. (Here the mode is three cases and the median too is three cases.) The defendant range is from no case through 15 cases.*

There exists a significant association between the rates of participation as plaintiff and rates of participation as defendant ($r_s = 0.69$, $P < 0.02$). Although exceptions are found (for example, the villager who was a plaintiff in ten cases and a defendant in only two cases, or the man who was a defendant in five cases but who never carried a complaint to the authorities) for the most part individuals highly involved in litigation tend to operate both as plaintiff and defendant. Some campesinos, on the other hand, manage to stay almost entirely clear of judicial involvements in any form.

*To save space I do not include here detailed tables giving the results of all statistical tests unless indicated otherwise in the text; all chi square analyses utilize cutting points as close to the

TABLE I Rates of Participation in Litigation

Number of cases	Number of subjects in sample		
	Plaintiff status	Defendant status	Total litigation
0	9	7	1
1	8	0	5
2	8	7	5
3	9	11	5
4	7	7	6
5	0	5	5
6	10	0	4
7	5	4	4
8	1	3	3
9	0	1	5
10	1	2	3
11	0	0	3
12	0	0	5
13	0	1	4
14	0	0	7
15	0	1	0
16	0	0	1
17	0	0	1
18	0	0	0
19	0	0	1
20	0	0	0
21	0	0	1

Perhaps the best technique for illustrating agonistic diversity in Incawatana and the range of intracommunity differentiation on aggressiveness is through the presentation of examples of abusive and of humble men and their behavior. First let us examine an example of a man considered abusive. Andres Quispe the individual with the highest rate of litigation. What were the acts which caused don Andres to spend so much time in the offices of the various village and district authorities? A sketch of his legal problems follows.

An Abusive Man: Andres Quispe

Over a 10 year period Andres was a principal figure in some 20 lawsuits most of them directed against him. He was called before the village authorities to answer such charges as the following:

- 1) sexually abusing his sister in law (April 1960)
- 2) inflicting a wound on a fellow villager (June 1960)

- 3) insulting and beating up his wife (December 1961)
- 4) violently threatening his wife (January 1963)
- 5) wounding an uncle in a brawl (July 1963)
- 6) failing to pay a debt (November 1964)
- 7) punching and kicking an aunt (July 1965)
- 8) attemptin_g to rape a neighbor's wife (September 1967)
- 9) enterin_g the compound of another aunt with the intention of stealing (February 1968)
- 10) insulting a fellow villager (December 1968)
- 11) insulting, injuring and stealing from an uncle (February 1969)
- 12) fightin_g with a woman he was trying to seduce (September 1969)
- 13) threatenin_g to kill his third wife (September 1970)
- 14) attacking and injuring his father (September 1970)

In a few cases Andres was the plaintiff too, charging others with having insulted and defamed him, having wounded him in fights, or having menaced his life.

Our information on a series of other problems which Andres has had is incomplete. It is said that he has had troubles with some neighbors over land, but we do not have adequate documentation of this conflict. However, as a consequence of the situation, Andres is reported to have cried (a means of gaining supernatural pity and favorable intervention) and cursed his neighbor, causing his premature death. Andrés's third wife has repeatedly consulted with district judicial authorities about the possibility of obtaining a divorce, but they tell her, "You are married, you cannot get divorced. Your husband could kill you, but you cannot separate because you are married." Some years earlier Andres had a disagreement with one of his uncles. To obtain vengeance, Andres stole the uncle's cow and tried to kill it, but it did not die. Instead it was found alive but bloody from wounds he had managed to inflict. There are gaps in our chronological record. These gaps are not due to periods of peacefulness; they correspond largely to times when Andres was absent from the community — see in Arequipa working.

By Incawatana standards, Andres is an abusive man, although not necessarily the most abusive man in the village, despite his extensive case record. His violence has had limits: he has not been implicated in homicide, while numerous co-villagers have been involved in that type of extreme aggression. But Andres moves from conflict to conflict, engaging in disputes with kinsmen, spouses, neighbors, and unrelated villagers. His behavior is not atypical.

Humble Men: Some Examples

Humble men are characterized by their low levels of participation in conflict, and this fact makes it more difficult to discuss them. However, some brief comments about several humble men are in order.

In Table I one notes that one individual had participated in not a single case of litigation. Several factors permit us to understand his non involvement. First, he spends at least half the year living outside Incawatana, returning to the community primarily to plant his fields and harvest them. Second, this man, Belizario, is an outsider (*forasteru*) born in a neighboring district and married outside Incawatana. Even decades of living in a Qolla community do not erase the edge that an individual is a *forasteru*.

Manuel and other humble men are not immune from provocations by aggressive co villagers. Manuel, for example, has been the victim of thefts on more than one occasion. In one instance, visitors to his house walked off with his personal papers and documents. His response was to inquire calmly of the visitors who had been to his house whether they had accidentally taken his papers. He had, of course. Many years before, too, someone had entered his house while he was absent, stealing a poncho, a carrying cloth, potatoes, and some household utensils. Manuel is certain that the thieves were kinsmen, but he did not sue because he lacked proof. Nor did he engage in acts designed to bring about redress or intervention because the value of his loss was not too high. Moreover, he would be too much bothered to be running around suing and entering into new conflicts. Manuel is a gentleman in Incawatana terms, a *kaballeru*, mild mannered and patient, neither quick to offend others nor readily provoked by the actions of others.

A second example of a humble man is Pablo Pacompia, a man in his forties and only a few years older than the abusive Andrés Quspe. For Pablo's records show only one case of litigation, and Pablo was the plaintiff. A neighbor, one of the most abusive men in the village with a reputation for being a trier of men, had entered Pablo's corral at night and had slaughtered Pablo's cow, worth approximately 1,100 soles. Pablo sued and recovered 130 soles in damages. His neighbor had reacted violently as a result of a minor disagreement between the two men.

A third example of a humble man, though not quite as humble as the two, is Antonio Parillo, who has been involved in some litigation, as follows:

- 1) He was sued for having captured a girl with whom he was having an affair; the matter ended in marriage.
- 2) He was one of seven members of a band, accused of stealing the mouth of an instrument belonging to one member of the band.
- 3) He was called to defend his wife, who was accused of stealing a neighbor's chicken.
- 4) He was sued by his brother-in-law for having gotten into a fight with him over a trivial matter while both were drunk.

Antonio has had no other serious conflicts or lawsuits. However, at the time of our field work was drawing to a close, a bit of trouble was brewing for Antonio.

His neighbor Cecilio Acuna (the same man as in Pablo Pacompia's case the cow killer and reputed three time human murderer) had begun to molest Antonio. Once while inebriated Cecilio had gone to Antonio's house and challenged him to a fight. Antonio, who was sober, declined. When sober he told us one must restrain oneself and not react emotionally to provocations. Trouble between Cecilio and Antonio seems to have developed because of a joking incident in which Antonio accidentally ripped the seam threads on Cecilio's poncho. Now Cecilio threatens to kill Antonio and he has challenged him to fight on several occasions. Antonio's response? And so now he has two offenses with me. On the third I shall sue him, probably before the authorities in Incawatana, to force him to give me a guarantee of safety and to obligate him to stop offending me. He enters right to my house. He is an assassin and surely he wants to do to me what he did to the others. He is crazy.

When asked why he had not been involved in more lawsuits Antonio replied 'One must be humble. One must not be a tough (macho) or anything. One should be humble. One loses money when one gets caught up in lawsuits and one loses time as well. Antonio's attitude is probably representative of the attitudes of the humble in Incawatana.

THE ABUSIVE VERSUS THE HUMBLE

The humble or nonaggressive men engage in fewer cases of litigation than do the abusive or aggressive ones ($\bar{x} = 5.6$ vs 8.3 cases, respectively, $\chi^2 = 8.48$, $P < 0.01$, $df = 1$, $n = 53$). Indeed, when one contrasts the highest with the lowest quartiles on the dimension of aggressiveness, the differences in litigation involvement are even more pronounced (as plaintiff $\bar{x} = 4.4$ vs 2.5 cases, as defendant $\bar{x} = 6.8$ vs 1.9 total litigation $\bar{x} = 11.2$ vs 4.4).

When one reviews the case histories of humble and abusive men and compares them, one finds a more basic difference than mere frequency of litigation. That difference is in the readiness to resort to violence.

Abusive Men Are Violent Men

Generally we find that humble men are drawn into conflict against their will by the actions of abusive ones. While we pointed out above that there is a positive association between rates of litigation as plaintiff and rates of litigation as defendant, another pattern must be mentioned. The abusive men, those high in aggression, tend to be involved in litigation more as defendants than as plaintiffs, and the humble men tend to be involved more as plaintiffs than as defendants. The abusers, men high in aggressiveness, are more likely to have a high ratio of defendant to plaintiff status than are humble men, those low in aggressiveness ($\chi^2 = 7.99$, $P < 0.01$, $df = 1$, $n = 53$). Humble men do not cause trouble, although sometimes they must react to the aggressiveness of others. When they react, they are more likely to depend on strategy (litigation) than on physical skill (violence).

Let us turn next to some hypotheses that might help us to understand causes of agonistic differentiation in Incawatana

SOCIAL SUPPORT AGGRESSION AND LITIGATION

In 1960 van Velzen and van Wetering showed an association between the relative peacefulness of a society and the presence or absence of fraternal groups. They hypothesized that aggressiveness is produced by groups of relatives pursuing their interests through conflict. Otterbein and Otterbein [1967] later confirmed the hypothesis that societies with fraternal interest are more likely to have feuding than societies without fraternal interest groups. An intracultural test of the van Velzen and van Wetering hypothesis is possible if the hypothesis is modified slightly.

The basis hypothesis which I set out to test is as follows: the larger the support set available to an individual, the more aggressive he will be. That is, conflict and aggression in Qolla society are instrumental rather than expressive; individuals with access to help (either in violent encounters or in litigation) will be more willing to engage in acts of aggression.

The social support set in Qolla society attaches to the household and consists primarily of the following categories of kinsmen and ritual kinsmen in relation to each adult member of the household: parents, siblings and their spouses; parents, siblings and their spouses; compadres and comadres; godparents and godchildren; sons and daughters and sons and daughters in law. Comparing the composition of social support sets is a rather complex task, which can be simplified only by making certain assumptions. In a manner similar to domestic groups and in coordination with individual life cycles, social support sets undergo a developmental cycle. As an individual ages, the size and composition of his or her social support set change. Households regularly add to their social support set through the establishment of ritual kin ties through birth and through marriage. At the same time they lose members of the set largely through death. The process is illustrated in Figure 1. The composition of the social support set of an old man is quite different from the composition of the social support set of a young man. The old man no longer has available his parents and godparents; he may have fewer living brothers and sisters (especially if he is a younger member of a sibling set) but will undoubtedly have numerous adult sons and daughters, sons in law and daughters in law, and godchildren and compadres. A young man, on the other hand, is likely to have his parents and parents in law, his siblings and their spouses and his godparents. But he will have few godchildren, no adult children or children in law, and few compadres.

Thus the age of the subject is a pertinent factor that enters into our calculations, especially since our subjects ranged from their early twenties to eighty-odd years. When necessary, therefore, in our analyses we shall control for age. In particular

Categories of Kin and Ritual Kin Supporters								
Age	Parents	Hair cutting and baptismal god parents	Uncles and aunts	Siblings	Offspring	Marriage god parents	Compadres	God children
20	+	+	+	+	±	—	—	—
30	±	±	±	+	+	+	±	±
40	—	—	—	±	+	±	+	+
50	—	—	—	±	+	—	+	+
60	—	—	—	±	+	—	±	+
70	—	—	—	—	±	—	—	±

Fig 1 Changes in Qolla social support sets during their developmental cycle (+ = present — = absent)

this must be done when using the aggressiveness variable since there is an association between age and aggressiveness (see below). The following tests deal with the size of particular segments of social support sets and with their total size. We assume that a relationship exists between the size of action sets (ie those actually mobilized) and the size of the pool from which individuals can be recruited for action sets. The success of recruitment efforts may vary in relation to a number of factors which have been presented by Gulliver [1971: 19–20]

Which members of his kin-set an individual can recruit perhaps in conjunction with a de facto leader other than himself depends on a number of considerations. First there is the nature of the interest for which the action-set is recruited: certain requirements, say homicide, can call for larger sets than others, say birth rituals for ego's child. Some members of the kin-set may recognize only certain obligations and not others. Secondly it depends on how far the interests of ego's kin are also involved and the advantages perceived by them. They may give help purely as an obligation to ego, with the expectation of obtaining reciprocal assistance in their future needs. But there are often other advantages and inducements: economic reward, co-operation with certain others among ego's kinsmen, political security or advancement, expression of opposition to someone who is ego's adversary and the like. Thirdly some kinsmen offer more useful assistance than others. In particular contexts some may be influential men, others may possess special ritual power or knowledge, or special skill, and others may have previous experience of some value in the matter in hand. Fourthly pressures of time and the claims of simultaneous interests of some potential recruits may preclude their inclusion at a particular time. Fifth, residential proximity

often makes it easier to recruit some kinsmen rather than others. The relative urgency of action may be important and the condition of communications. Sixthly, the actual state of interpersonal relations between ego and each of his kinsmen individually may affect recruitment: he is likely to appeal and with more success to those with whom he is more friendly or to whom he has given generous assistance. Some kinsmen may have or feel that they have a greater obligation to accede to his request. Seventhly, the *de facto* leader of the action-set, if different from ego, may for any of the previous reasons attract or deter potential recruits.

These considerations are applicable to the Qolla case. To give one example, the reader will recall that Andres Quispe's aggressiveness was on many occasions directed against members of his social support set, and it seems reasonable that those individuals are not likely to provide Andres with help when he needs it. For practical reasons (e.g. lack of sufficient data on many of these points) we must make the assumption of a high correlation between the size of social support set and the possibilities of recruitment for action sets.

We must make another assumption, too. The indicators of aggressiveness and litigiousness correspond to a ten year period. But in the calculations of partial total social support sets we have used the figures which correspond to the date of our census, 1969. We assume that the rates of change do not differ for individuals high and low in aggressiveness and litigiousness, even though there may be differences in absolute size.

Ideally, members of an individual's social support set should come to his assistance when he is in trouble. If he gets into a fight, they should fight also or try to stop the fight. They should lend support in hearings before the authorities. When his time is taken up with serious cases, they should volunteer to work his fields. In instances of serious conflict among the Qolla, self-help activities are important. [Bolton 1970]

The first hypothesis that we tested was derived from the van Velzen and van Wetering hypothesis. We predicted that subjects with a larger number of living brothers would be more aggressive than subjects with few or no living brothers. The results indicate that there does not exist an association between the number of living brothers and level of aggressiveness (high aggressors = 1.6, low aggressors = 1.5, $P = NS$). If one uses an age-controlled sample (since number of living brothers is an age-related variable) then a statistically significant relationship emerges when one considers those who have a living brother versus those who have no living brother (see Table II). This finding could be interpreted as providing some slight support for the social support or fraternal interest group hypothesis, since this division into those with a brother versus those without a brother corresponds to the presence versus absence of fraternal interest groups. However, other interpretations of this relationship could be advanced.

TABLE II Number of Living Brothers and Aggressiveness

Number of living brothers	Aggressiveness	
	High	Low
None	2	9
One or more	25	17

$\chi^2 = 5.95$ $P < 0.02$ (age-controlled sample)

- 1) The reputation for aggressiveness might be gained because of fighting among brothers thus possibility too would seem to fit with the fact that the break comes between no brothers and one brother
- 2) The presence of brothers offers possibilities for training in aggressiveness during childhood
- 3) Differences in sibling set composition may be associated with differences in childrearing experiences and therefore aggressiveness

If the social support hypothesis is the correct interpretation of the association then we reason this relationship should hold up — indeed be stronger — when we use litigation rates as the dependent variable. After all it is in litigation and in the forms of aggression that lead to litigation that social support is of greatest utility. But regardless of whether one uses the complete sample or the age controlled one a relationship between litigation and number of living brothers is nonexistent although it should be pointed out that there is a slight tendency which is not statistically significant for subjects with no living brothers to engage in more total litigation a similar tendency approaches significant levels when one considers litigation as plaintiff separately ($\chi^2 = 2.76$ $P < 0.10$ $df = 1$ $n = 53$). The fact that subjects with no living brothers may be more willing to take complaints to judicial authorities may indicate a willingness on the part of villagers to act aggressively toward individuals without a significant support set without a fraternal interest group. Having living brothers may serve as a deterrent against attack and thereby lower involvement in litigation. When we examine rates of litigation as defendant we find no relationship whatsoever with the number of living brothers. If those with brothers are more aggressive than those without brothers then having brothers may also protect them from litigation as defendants the injured party may be more reluctant to sue an opponent who has a male sibling. What is troubling about these findings is the fact that they apply not to the number of living male siblings but only to the case where there is one or more versus none. If this line of thought were correct then the results should emerge

also when the independent variable is continuous rather than dichotomous? If this is not the case we conclude that the social support hypothesis with respect to living male siblings receives minimal support at best.

What can be said about the other interpretations of the association between presence of a living brother and aggressiveness? We believe that the third interpretation offers the greatest promise — i.e. that differential socialization experiences are involved. Where one finds large sibling sets one is likely to find less attention and care devoted to each child. Physical punishment is more likely to occur in smaller families [Bolton and Bolton 1972]. These factors should lead to increased aggressiveness. One way to test this interpretation is through an examination of birth-order data. In Qolla society preferential treatment is accorded to the first born child especially a male and a male last born child. There exists a statistically significant relationship between birth order and aggressiveness: first and last born males are less aggressive than middle born males. (Since age and birth order are unrelated phenomena we have used the complete sample to test this hypothesis.) In Table III we present the pertinent data. Birth order and litigiousness are not associated in this sample.

In addition to this work on the number of brothers a systematic and thorough search for associations between other segments of social support sets and aggressiveness and litigiousness was carried out. Specifically we attempted to find correlations between the dependent variables and the number of ego's living female siblings (maximum 6 minimum 0) of sons 15 years old or older (4/0) of daughters 15 years old or older (5/0) of total living offspring 15 years old or older (8/0) of compadres chosen for ego's children's haircutting (11/0) baptism (11/0) and marriage (10/0) of compadres who chose ego to serve as godfather for their children's haircutting ritual (9/0) baptism (6/0) and marriage (9/0) the total number of times ego was chosen to be a godfather (15/0) and the total number of times ego chose others to become a compadre (28/2). Relationships were also sought with whether or not ego's and his wife's parents and godparents were still living (each type tested individually). Finally correlations were sought with figures calculating the size of ritual kin sets for ego and his wife (they ran in size from a maximum of 40 to a minimum of 7) the size of ego's kin set — i.e. offspring, parents and siblings (maximum 22 minimum 3) — and the size of the complete social support set — i.e. a combination of the kin set and ritual kin set (maximum 61 minimum 18).

It is clear that as a result of demographic processes (largely though not exclusively) there exists considerable differentiation with respect to the amount of support a person in Incawatana might possibly mobilize in time of trouble. Yet the results of our search were overwhelmingly negative. That is there were only five significant relationships ($P < 0.05$) of a total of 104 tests and even these findings which in any event simply reflected what one might expect by chance were not in a direction that would favor the social support hypothesis.

TABLE III Birth Order and Aggressiveness

Birth order	Aggressiveness	
	High	Low
First or last child	9	17
Middle child	24	14

$$\chi^2 = 5.02 \quad P < 0.05$$

Consequently it seems reasonable to conclude that the social support hypothesis does not succeed in explaining differences in aggressiveness and litigiousness in the Qolla context. Although failure to find support for the social support hypothesis can be viewed as evidence in favor of the supposition that Qolla aggressiveness and litigiousness are not highly instrumental, it is possible of course that the failure simply means that potential support from kinsmen and ritual kinsmen does not enter into the instrumental calculus employed by Qolla men before engaging in agonistic behavior. Other social and economic factors may be important nonetheless and before deciding that instrumental aggression is insignificant it might be best to examine relationships between social status dimensions and aggressiveness and litigiousness.

SOCIAL STATUS AGGRESSION AND LITIGATION

The second set of hypotheses that we tested involves social status. To what extent is status differentiation or status inequality related to differential aggressiveness and participation in litigation? From a variety of theoretical perspectives (eg. frustration-aggression theory, relative deprivation theory, and the hypoglycemia hypothesis) one would tend to predict an inverse correlation between aggressiveness and social status. On the other hand, if Qolla aggressiveness and litigiousness are instrumental and have adaptive consequences for the individual permitting him to gain access to valued resources, then we should find positive relationships between aggressiveness and litigiousness and social status. To complicate the problem, of course, forces could be operating from both directions in which case we should expect no relationship whatsoever between some indicators of status (eg. wealth) and aggressiveness or conceivably a bimodal distribution with individuals at both ends of the status continuum rated as highly aggressive, the aggression of the poor being largely expressive and the aggression of the rich being instrumental.

Taken together the following elements define in great measure the social standing of adult males within Incawatana: 1) wealth, 2) education, 3) age, 4) participation in communal rituals, and 5) participation in the political life of the community.

in more total litigation than did less highly educated subjects ($r_s = 0.61$ $P < 0.01$) and the more highly educated men were more likely to be involved in litigation as plaintiffs than were the less highly educated men ($r_s = 0.60$ $P < 0.05$). Rates of litigation as defendant though were unrelated to educational attainment.

These findings suggest that while education has no influence on aggressiveness it may predispose individuals to seek redress for perceived wrongs through judicial proceedings. It is likely that education equips the Qolla villager with a better understanding of the legal system, enhances his confidence in his ability to utilize the system (if only because of the increase in knowledge of Spanish gained in school) and improves his strategic competence. Conceivably he initiates more litigation because his higher status per se raises the chances of a favorable outcome; he can obtain his objectives more readily through litigation than through other means more likely to be perceived as aggressive. The more educated individual engages in neither more nor less behavior of a type which is likely to result in his being sued, or if he does engage in more such behavior than does a less educated person, he is more successful at avoiding the legal consequences.

The Age Factor

Although there are no special perquisites accruing to the aged and no council of elders at the village level in Incawatana, increasing years do bring with them an increase in status, general respect and some ceremonial deference. This is true as long as aging is not accompanied by a decrease in other components of status; for instance, in wealth, a poor old man is not likely to enjoy high status.

Our analysis suggests that aggressiveness declines with age to some extent ($r_s = 0.30$ $P < 0.02$). However, litigiousness is not significantly related to age. Old and young were involved equally in litigation as plaintiffs, as defendants and as a whole.

The Ritual Factor

The religious cargo system in Incawatana is complex and cannot be described in detail in the present context. Sponsors are required for various fiestas in the yearly ritual cycle; indeed, most fiestas include multiple events each requiring one or more sponsors. The major periods when sponsors are called for include Carnival, Holy Week, and the fiesta of the patron saint of the community. The sponsors may pay for the Mass, for dance groups, for expenses associated with the raising of altars, for decorating images of the saints, and for fireworks displays. Most sponsors, of course, must also entertain the retinue of relatives and friends who aid them in carrying out their duties. Cargos vary in expensiveness and prestige and normally a cargo career involves starting with the less costly and less prestigious cargos and proceeding to those higher in rank. Most individuals participate in the cargo system since participation is expected, particularly of those who have accumulated some wealth. Pressure is exerted on community members who fail to volunteer for a cargo if it is felt that they are capable of handling

1 bility. Participation in the cargo system is necessary though not sufficient to attain and maintain high status.

To operationalize the ritual participation factor we have tabulated the number of cargos held by an individual without attempting to rank them. Efforts to discover statistically significant associations between ritual participation on the one hand and aggressiveness and litigiousness were unproductive. At most there appears to exist a slight tendency for individuals high in ritual participation to engage in more total litigation and more litigation as plaintiff than do individuals low in ritual participation.

The Political Factor

The political structure of Incawatana contains a large number of authority positions: *teniente*, *alcalde*, *segunda jilacata*, school board, graveyard keeper, and others. Some positions have more than one occupant; for example, there are at any one time several *tenientes* in Incawatana.

Occupancy of most of these positions is of limited duration and tends to rotate among interested and willing adult males. While some men never accept public positions, others serve in one position or another repeatedly. There exists the risk of over involvement in the political life of the community: a man who appears too eager to serve as *teniente* and too often is suspected of wanting the post in order to enrich himself from the fees paid for settling disputes. But on the whole, having served as an authority adds to an individual's status. While the villagers of Incawatana tend not to display a high degree of respect for office holders (indeed at times they would seem to enjoy defying the authorities), men are proud to claim having held such and such position.

Political participation was operationalized by counting the number of political posts an individual had held during his lifetime; this varied from none to five. Although there were trends indicating that political participation was associated positively with litigiousness and aggressiveness, the results were not statistically significant. But attention should be directed to one important finding. All nine individuals in our sample who had served in the post of *teniente*—the position with the most prestige and power—were considered high in aggressiveness (binomial test, $P < 0.002$). The interpretation of this finding is problematic, since several possibilities come to mind. It is conceivable that only the more aggressive men in the community are willing or able to function in the role of *teniente*, which is one that requires the holder to become involved in the conflicts of fellow villagers in order to try to resolve them. Or perhaps, having served as a *teniente*, these men are perceived as more aggressive because of the role they had to play while an authority. Finally, it is possible that having to be aggressive to perform as *teniente* may lead to a continuation of such behavior even after the person no longer holds the position. As might be expected because of their above average familiarity with the judicial system, *tenientes* tend to engage in more personal litigation than do those who never served as *teniente*, but these findings are not statistically significant.

The Social Status Index

In order to arrive at an overall assessment of the relationship between social status and aggressiveness and litigiousness it was necessary to construct a social status index incorporating information from the five main components of status identified earlier — ie wealth age education ritual participation and political participation. Such an index was devised by assigning to each subject a score of from one to four on each of the five separate status components according to the attributes the subject possessed on a given indicator. The maximum score obtained on this index (highest status) was 18 and the minimum score was 7 (lowest status). Using this approach no association is found between social status and aggressiveness but there is a positive correlation between social status and litigiousness as plaintiff ($r_s = 0.69$ $P < 0.05$) and total litigation scores ($r_s = 0.62$ $P < 0.05$).

SUMMARY AND CONCLUSION

In this paper we have explored the relationships between agonistic behavior and social phenomena in an effort to determine whether such behavior among the Qolla is instrumental in character. Two different measures of agonistic orientation were used one of these which we have labeled aggressiveness is based on key informants ratings of the extent to which men in the sample of adult males from Incawatana engaged in fighting violence and other actions intended to be harmful to an opponent the second agonistic measure is litigiousness which involves the frequency of involvement by these same men in litigation over a ten year period.

The pattern of results strongly suggests that aggressiveness and litigiousness while certainly related to each other are conceptually distinct. The highly aggressive individuals tend also to be highly litigious to be sure but significantly they tend to be particularly involved in litigation as defendants (rather than as plaintiffs) even though there is a positive association between rate of involvement by individuals in litigation as plaintiffs and as defendants.

The social support hypothesis did not fare well in relation to agonistic behavior. With one possibly meaningful exception neither litigiousness nor aggressiveness seems to be influenced by the availability of potential supporters that is people bound to ego by bonds of kinship or ritual kinship. While prejudicial to the social support approach to agonistic behavior these findings are not surprising. They provide confirmation of the assessment that Qolla society is atomistic [Rabold and Kupferer 1968] and that solidarity even within the nuclear family tends to be fragile [Bolton and Bolton 1975]. An individual cannot count on others for support in a crisis. Indeed those who should provide support who are morally required to help because of kinship and compadrazgo ties may be the very one with whom an individual is engaged in struggle.

The exception mentioned earlier as an instance of possible evidence favoring the social support hypothesis however attenuated involved the existence of a male sibling since having a brother was associated with higher levels of aggressiveness in our subjects. That a similar finding did not emerge with respect to litigation raises important issues of interpretation. After all, fraternal interest groups could use judicial processes too to further their instrumental goals. Lawsuits brought before the village authorities are occasions for acrimonious and emotional debates between opponents and persons other than the primary parties are allowed to join in the proceedings the outcome of which might be influenced by the numbers present on each side. An additional problem for the social support interpretation of the relationship between fraternal presence and aggressiveness is the fact that the size of the fraternal group is irrelevant — ie shows no correlation with aggressiveness. Thus it seems plausible that if the association between the existence of a brother and aggressiveness is not merely fortuitous causes unrelated to the social support dimension might be involved for example differential socialization practices associated with birth order and sibling set size and composition. Although it was beyond the scope of the present paper to test this alternative thoroughly some available information suggests that socialization effects mediated by birth order might be operative.

Failure to replicate a cross cultural finding at the intracultural level may or may not be significant [Shweder 1976] but given the above results we would like to raise the possibility that the research which prompted the present investigation (ie that of van Velzen and van Wetering [1960] and that of Otterbein and Otterbein [1965]) might be profitably re-examined. These scholars used residence patterns to index fraternal interest groups (present they suggest in patrilocal societies). The Otterbeins also used polygyny to index fraternal interest groups. But are these two indicators not also associated with differential socialization practices eg father absence in the case of polygyny? Bacon et al [1963] have demonstrated a correlation between mother-child sleeping arrangements and personal crimes. Further confirmation was provided by B Whiting [1965]. Then too polygyny and patrilocality are associated with diets low in protein [J Whiting 1964] and we would like to suggest therefore that as a consequence of hypoglycemia induced by a protein deficient diet and associated stressors these societies might have higher levels of irritable aggressiveness [see Bolton and Vadheim 1973]. The aggressiveness produced by physiological factors and by socialization practices could be responsible for the failure to develop political institutions which could if present control feuding. This alternative to the fraternal interest group hypothesis merits testing.

Turning to other social factors it could be argued that social status might affect aggressiveness in various ways [Pertti and Gretel Pelto personal com

munication] For example poorer individuals might be likely to engage in behavior seen as aggressive in order to acquire resources needed for their survival the less educated men may be less cautious about their behavior less capable of genteel management of interpersonal relations and therefore more likely to be judged aggressive by their peers However as report above aggressiveness was not associated with overall social status or with three of the separate indicators of status wealth education and ritual participation Understandably in biological terms there was a negative association between age and aggressiveness And to some extent there appears to be a positive association between politico juridical participation and aggressiveness men who serve as authorities being more likely to be viewed as aggressive With additional information it is difficult to sort out the direction of causality in the relationships involved in this specific finding

Our findings in regard to social status variables and litigiousness are almost reverse of those with aggressiveness The more highly educated subjects do enter in more total litigation and more litigation as plaintiff than do the less educated ones Education may indeed incline an individual to respond with more restraint to provocations and to utilize judicial processes to attain goals The positive association between wealth and litigiousness both total and as plaintiff may stem from an ability to pay and perhaps too from the fact that those with proper resources are more likely to experience damages some of which might be produced accidentally and others inflicted intentionally from envy (*envidia*) Litigiousness appears to be unaffected by age and ritual participation and only minimally so by politico participation (if at all)

On the basis of this analysis I would conclude that social support factors do not explain differential aggressiveness and litigiousness among the Qolla and further that their irrelevance gives additional strength to previous conclusions concerning the biological and expressive nature of this aspect of Qolla behavior At the same time this analysis allows us to see that other social and economic factors while not implicated in aggression per se are related to responses to aggressive behavior specifically to the resort to judicial processes People high in social status in wealth and education are most likely to initiate legal proceedings. This while aggressiveness is minimally instrumental litigiousness may indeed be heavily governed by instrumental considerations in Qolla society

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Centrally Elicited Aggressive Behavior A Model System for the Study of Episodic Neurobehavioral Pathologies?

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Studies in which the predatory like attack of a cat upon a rat has been elicited by electrical brain stimulation have been briefly reviewed with an emphasis on the question of where within the central nervous system such brain stimulation is producing its behaviorally meaningful effects. Two opposing but by no means mutually exclusive views are considered. The first is that brain stimulation elicits this behavior pattern primarily because it affects a specific motivated behavior system that is organized discretely in the midbrain and pons. The second is that forebrain neural activity is modulated in behaviorally significant ways by brainstem stimulation which elicits predatory like aggressive behavior in the cat.

The possibility that further research on the altered state of central nervous system activity induced by brain stimulation which elicits aggressive behavior in the cat may lead to a further understanding of the altered states of central nervous system activity that underlie the aggressive dyscontrol syndrome and other episodic state disorders is discussed.

Key words: aggression predation episodic neurobehavioral disorders hypothalamus brainstem electrical brain stimulation cat

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INTRODUCTION

Much of clinical psychiatry — particularly in the more severe disorders characterized by intense discrete behavioral patterns that are to varying degrees reversible and separable clinically and therapeutically from long term personality traits which may characterize the steady state behavior of patients. Episodes of aggressive dyscontrol as well as severe depression manic overactivity or psychotic ideation are clearly due to altered patterns of central nervous system activity. They are patterns in that they are reversible and no known structural abnormalities can usually be demonstrated. Although the neural substrate vulnerability underlying any of these conditions is unknown the result is that the central nervous system is captive to abnormal behavioral programming processing of sensory information is biased flexibility in interpretation and response is lost basic central functions such as sleep and appetite are altered the content of subjective experience is determined by the form of the patterns of central nervous system dysfunction.

In the attempt to understand the changes in central nervous system activity that underlie such behavioral state changes one of the most significant developments of the last decade has been an appreciation of the extent to which the functional state of the entire forebrain is dependent on the level of neural activity in various lower brainstem cell groups. The suggestion 10 to 15 years ago that alterations in neural activity of small groups of brainstem neurons (e.g. locus coeruleus midbrain raphe) could monosynaptically affect the neural activity of the entire cerebral mantle would not have been taken seriously. Now it is accepted that at least several lower brainstem neuronal groups possess this capacity. The potential significance for altering all aspects of cortical functioning including those mental functions unique and most significant to man is profound. One of these groups especially the monoaminergic ones have been subjected to intensive investigation and theories of affective disorders and schizophrenia have been proposed. However because of the very general breadth of effects that follow manipulation of monoamine systems (practically all behaviors in which organisms can engage are affected) the answer to one of the critical questions — in what way do such cell groups alter forebrain neural activity to produce the specific aberrant patterns of behavior we describe as aggressive manic depressive or psychotic? — is unlikely to come solely from this avenue of research. The discovery of other brainstem neuronal groups that influence the neural activity of the forebrain but in ways that impose specific coherent behavior patterns would be an important advance. Their study could contribute to our general understanding of how ascending modulatory systems produce the patterns of central nervous system dysfunction that underlie the different episodic behavior disorders. In this regard recent research which has found that electrical stimulation of discrete

areas in the midbrain [Bandler 1975 1977 Bandler et al 1972 Proshansky and Bandler 1975] and pons [Berntson 1973] elicits a well integrated predatory like attack by a cat upon a rat may be important

CENTRALLY ELICITED ATTACK BEHAVIOR

Parallels between the altered states of central nervous system activity that underlie certain episodic behavior disorders and the altered states of central nervous system activity induced by brain stimulation that elicits aggressive behavior in the cat have previously been noted [Bowers 1974]. These relate to similarities in terms of stimulus input biasing and to limitations in the flexibility of the response because they have been reviewed elsewhere [Bowers 1974 Flynn 1976 Flynn and Bandler 1975 Flynn et al 1971] together with the important evidence that the effects of unilateral brain stimulation that elicits attack are largely lateralized within the central nervous system they will not be discussed further here. Instead we will focus on the question of where within the central nervous system such brain stimulation may be producing its behaviorally meaningful effects.

The hypothalamus has long been central to all theorizing on the neural basis of this behavior. I think there are at least two reasons for this. First the hypothalamus is known to be important for autonomic-endocrine-emotional adjustments and is a central structure through which the limbic system affects behavior in these spheres. Second the lateral hypothalamus was the first region in which stimulation was found to elicit predatory like behavior [Wasman and Flynn 1962]. Yet as far back as 1968 Ellison and Flynn showed that after surgical isolation of the hypothalamus cats could still be motivated to show natural predatory behavior and predatory like attack behavior could still be elicited by stimulation of the midbrain reticular formation. Since natural and centrally elicited predatory behavior were present in a brain with a neurally disconnected hypothalamus this study quite convincingly demonstrated that the hypothalamus is not concerned with the organization of this behavior pattern but rather with the modulation of other areas in the brain where the behavior must be organized.

There is no shortage of such areas. In the 15 years since the behavior was first discovered forms of predatory like attack behavior have been reported during stimulation of the posterior midline thalamus [Bandler and Flynn 1974 MacDonnell and Flynn 1968] the preoptic region [Bandler 1979 Inselman and Flynn 1972] the midbrain ventral tegmental area [Bandler et al 1972 Proshansky and Bandler 1975] the midbrain reticular formation [Sheard and Flynn 1967] the rostral midbrain dorsal periaqueductal gray substance [Bandler and Flynn 1974] the caudal midbrain supratrochlear periaqueductal gray substance [Bandler 1975 1977] the dorsolateral pontine tegmentum [Berntson 1973] and the fastigial nucleus of the cerebellum [Reis et al 1973] (see Figs 1-3).

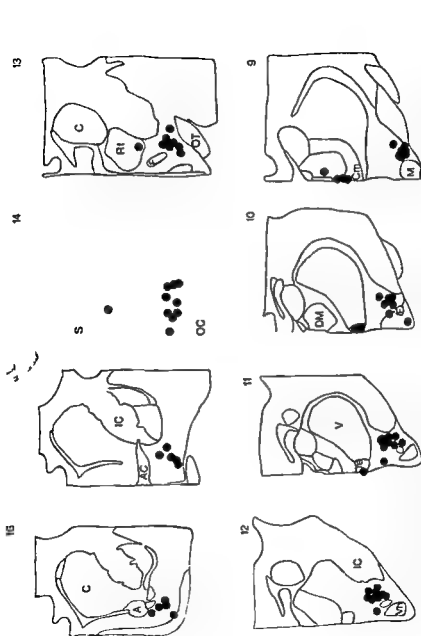


Fig. 1. Map of preoptic hypothalamic and thalamic points from which pr. datory attack has been elicited by electrical stimulation. In the rat, compiled from Bandler [1979], Flynn [1967], Lerman and Flynn [1972], MacDonnell and Flynn [1968], Siegel and Ciba [1971], Siegel [1972], and Wynn and Wynn [1962]. Symbols: S, substantia nigra; OC, olivary complex; IC, internal capsule; AC, anterior commissure; DM, dorsal medial nucleus; V, ventral nucleus; A, anterior nucleus; C, caudate nucleus; RI, rostromedial nucleus; OT, olivary tubercle.

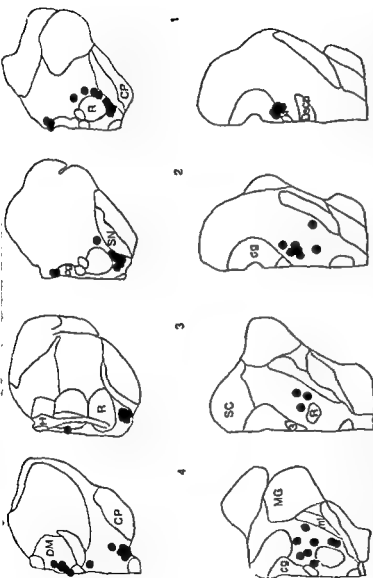


Fig 2 Map of thalamic and midbrain points from which predatory attack has been elicited by electrical stimulation in the cat. Compiled from Bandler [1975, 1977], Bandler et al [1972], Bandler and Flynn [1974], Flynn [1967], MacDonnell and Flynn [1968], Sheard and Flynn [1967], and Wasman and Flynn [1967]. Sections are drawn according to the atlas of Jaxer and Aymone-Marxan [1954]. Anterior frontal plane for each section is in the upper right corner. Abbreviations: CP cerebral peduncle, Decp decussation of superior cerebellar peduncle, DM dorsomedial nucleus of thalamus, MG medial geniculate nucleus of thalamus, R red nucleus, SC superior colliculus, SN substantia nigra, cg central gray substance of midbrain, ml medial lemniscus, 3 oculomotor nucleus, 4 trochlear nucleus.

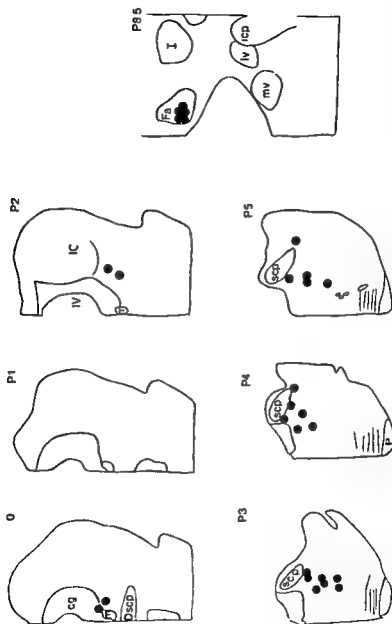


Fig. 3. Map of pontine nuclei of the rat brainstem. The diagrams show the location of the nucleus reticularis (R) in various sections. The diagrams are labeled P0, P1, P2, P3, P4, P5, and P85. The diagrams show the brainstem in cross-section with various nuclei labeled: IC, IV, ICp, mv, I, Fa, cg, and R. The R is shown as a cluster of black dots. The diagrams are arranged in two rows: P0, P1, P2 on the left and P3, P4, P5 on the right, with P85 at the bottom center.

DESCENDING ORGANIZATIONAL MODEL

Of all these sites the discovery of several discrete regions in the midbrain and pons deserve particular attention

It has been known for some time that the presence of large lesions of the anterior hypothalamic preoptic region [Bergquist 1970] or surgical isolation of the hypothalamus [Elison and Flynn 1968] do not eliminate the attack elicited by lateral hypothalamic and midbrain reticular formation stimulation respectively whereas small lesions in the midbrain ventral tegmental area [Proshansky and Bandler 1975] or large lesions made in the midbrain reticular formation [Berntson 1972] eliminate hypothalamically elicited attack behavior. In addition, while electrical stimulation of preoptic hypothalamic midbrain and pontine regions elicit predatory like attack behaviors that are seemingly identical in form and target selectivity, much higher intensities of stimulation are required to elicit the behavior with preoptic or hypothalamic stimulation than with midbrain or pontine stimulation [Bandler 1977, 1979; Proshansky and Bandler 1975] (see Fig. 4).

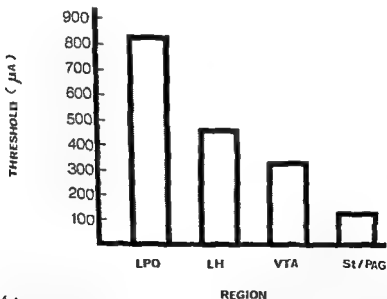


Fig. 4 Average minimum intensity of stimulation required to elicit attack upon a rat in less than 15 seconds for five of six trials on each of three days. Compiled from Bandler [1975, 1977, 1979]. Each average minimum intensity is derived from individual thresholds for no fewer than 18 electrodes in each region. Intensity of stimulation data was not reported for pontine tegmental attack sites [Berntson 1973] but Berntson (personal communication) has indicated they are comparable to those in the St/PAG region. Abbreviations: LPO, lateral preoptic region; LH, lateral hypothalamus; VTA, ventral tegmental area of midbrain; St/PAG, supratrochlear periaqueductal gray region.

Taken together these studies have led many to the conclusion that neuronal groups in the midbrain and pons organize this behavior and that it is these regions which in turn are modulated by stimulation of the rostral brainstem (ie preoptic region hypothalamus and thalamus) [Bandler and Flynn 1974 Bergquist 1970 Bertson 1972 1973 Chu and Flynn 1971 Chu et al 1976 Flynn 1976] While this view may yet prove to be substantially correct the data are by no means unequivocal

ASCENDING MODULATORY MODEL

The problems with what we can perhaps call the descending organizational model of centrally elicited aggressive behavior in the cat are as follows First several recent studies [Bandler 1975 1977 1979 Bandler and Fatouns 1978 Proshansky and Bandler 1975] have drawn attention to the fact that there are almost certainly large regional differences in the configuration of the common neuropil likely affected by stimulation in the preoptic region lateral hypothalamus and midbrain ventral tegmental area — the medial forebrain bundle — and that the differential effectiveness of lesions in the anterior hypothalamic preoptic region versus those in the midbrain region may simply be due to the greater compactness of the medial forebrain bundle in the caudal region Thus even large anterior hypothalamic preoptic region lesions are ineffective perhaps because they are less likely to destroy neuropil in common with other lateral hypothalamic attack sites than are small ventral tegmental area lesions The different results of lesions in these regions then may tell us nothing about the directionality of stimulation effects Second so similar are the attack behaviors elicited by stimulation of different regions (preoptic region lateral hypothalamus midbrain ventral tegmental area midbrain supratrochlear central gray area pontine tegmentum) [Bandler 1977 1979 Bertson 1973] that it is probable that the stimulation is affecting a common neural substrate Yet the known anatomical interconnections of these areas do not suggest such a common descending neural substrate The only study [Chu et al 1976] that has specifically examined this question failed to find any significant anatomical projections from the three interconnected [Chu and Flynn 1971] attack-eliciting rostral brainstem regions (preoptic region hypothalamus midbrain ventral tegmental area) to the two known attack-eliciting caudal brainstem regions (supratrochlear central gray area pontine tegmentum). This is all the more significant as the attack threshold stimulation intensity data suggest that there should certainly be substantial convergence of the descending projections from the relevant rostral brainstem regions onto the relevant caudal brainstem regions The only known common neural substrate linking these five regions is the *ascending* medial forebrain bundle Finally in a recent study Bertson et al [1976] drew attention to the extent to which the predatory behavior elicited by brain stimulation resembles natural predatory behavior of cats

are tested with live rats in a naturalistic environment. For example, in such an environment stimulated cats will use their paws to drive a live rat from behind an obstacle that makes it impossible for the cat to bite the rat. Such complex intentional behavior would seem to require that the brain stimulation modulate forebrain as well as brainstem neural mechanisms. Just that has in fact been proposed. In a review Siegel and Edinger [1978] concluded that the stimulation that elicits attack must ultimately produce altered pattern of neural activity in parietal, temporal, and frontal neocortices. If this proves to be substantially correct, stimulation of the rostral brainstem (preoptic region, lateral hypothalamus, midbrain, ventral tegmental area) may well alter cortical neural activity via effects on components of the ascending medial forebrain bundle. Ascending pathways other than those within the medial forebrain bundle would likely be involved in the effects of stimulation in other regions, as we have already noted the finding that midbrain reticular formation stimulation (not to be confused with midbrain ventral tegmental area stimulation) elicits attack after surgical isolation of the hypothalamus [Ellison and Flynn, 1968].

TWO MODELS, QUESTIONS AND SPECULATION

The discovery of discrete regions in the lower brainstem at which low intensities of stimulation elicit a complex motivated behavior then serves to focus attention on a most important question: Does brain stimulation elicit this behavior pattern primarily because it affects a specific motivated behavior system that is organized discretely in the midbrain and pons? Or is forebrain neural activity modulated in behaviorally significant ways by the brainstem stimulation that elicits predatory aggressive behavior in the cat? If the latter, what determines the form of the elicited behavior: the stimulated modulatory system(s) or the function of the affected forebrain regions? We do not know the answers to these questions, but they are important with respect to the general significance of the centrally elicited predatory attack model.

The concept that the central nervous system possesses some kind of latent capacity for patterns of functioning (or dysfunctioning) that underlie the aggressive dyscontrol syndrome(s) and other episodic state disorders is central to all theorizing on the biological bases of mental illness. Electrical stimulation of the brain then offers one method of revealing certain of these capacities, including perhaps capacities thought to be uniquely dependent on forebrain neural tissue. In this regard, the fact that stimulation of certain lower brainstem regions in the cat elicits a predatory-like aggressive behavior may be misleading. It is worthwhile, I believe, to remember that the cat is a carnivore and the product of a unique evolutionary history. Because the cat is a mammal, nowhere would we expect the effect of that history to be reflected in central nervous system development more than in the development of the forebrain. It would not be any more surprising then to

find that alterations in the neural activity of brainstem cell groups that project to widespread regions of the forebrain in the cat would affect predatory behavior than to find that manipulation or abnormal functioning of the same brainstem neuronal groups in man could alter mental functions or consciousness. In the two species comparable patterns of altered forebrain neural function could well produce alterations in different behaviors.

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Predatory Attack Behavior in the Cat Elicited by Preoptic Region Stimulation A Comparison With Behavior Elicited by Hypothalamic and Midbrain Stimulation

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The predatory attack of a cat against a rat elicited by preoptic region lateral hypothalamic and ventral midbrain stimulation has been compared. Regardless of the region stimulated the attack behaviors were found to be nearly identical with respect to response topography preference for the rat as an attack object the distance at which the cats would approach and attack a rat and the success in finding and attacking the rat when the cats were blind folded. However the minimum current required to elicit the predatory attack by preoptic region stimulation was two to three times greater than that required to elicit the same behavior by lateral hypothalamic and ventral midbrain stimulation. It was considered that the medial forebrain bundle is likely to provide the common neuropil affected by stimulation in each region and that its differing regional density may explain the results.

Key words: aggression, predation preoptic region hypothalamus midbrain electrical brain stimulation cat

INTRODUCTION

Wasman and Flynn [1962] first reported that electrical stimulation of the lateral hypothalamus of the cat elicited a quiet predatory like biting attack on a rat. Since then it has been found that electrical stimulation of many other regions of the central

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nervous system elicits similar forms of behavior: posterior midline thalamus [Macneil and Flynn 1968, Bandler and Flynn 1974], preoptic region [Inselman and 1972], midbrain ventral tegmental area [Bandler et al 1972, Proshansky and Bandler 1975], rostral midbrain dorsal central gray substance [Bandler and Flynn 1974], midbrain reticular formation [Sheard and Flynn 1967], caudal midbrain supraolivary central gray substance [Bandler 1975, 1977], central pontine tegmentum [Inselman 1973], and fastigial nucleus of the cerebellum [Reis et al 1973]. This multiplicity of sites from which predatory like behavior can be elicited indicates that the elicited behavior has a quite widespread and complex neural organization within the brain. An understanding of the neural relations of the regions from which such attack behavior can be elicited would seem to be essential if we hope to understand where within the central nervous system the electrical stimulation is having behaviorally meaningful effects. A first step is to compare the behaviors elicited by stimulation of different regions of the brain.

It is generally accepted that quiet biting attack elicited by stimulation of the lateral hypothalamus and ventral tegmental area of the midbrain is dependent on the existence of a common neuropil — the medial forebrain bundle [Proshansky and Bandler 1975, Flynn 1976, Chu et al 1976, Bandler 1977]. Rostrally the medial forebrain bundle occupies a large cross-sectional area of the preoptic area, a region from which a quiet predatory like attack behavior has been elicited [Hutchinson and Rendrew 1966, Inselman and Flynn 1972]. For this reason we thought that a comparison of the attack behavior elicited by stimulation of the preoptic area, lateral hypothalamus and midbrain ventral tegmental area could likely provide important information about the relationship of these attack-eliciting regions as well as about the functional organization of the medial forebrain bundle with respect to this form of aggressive behavior.

METHODS

Initial observations were made on 27 cats (15 females, 12 males) at least one week after they arrived in the laboratory to determine if any of them spontaneously attacked rats. This was tested on each of 3 days by placing the cat for 2 hours in a test cage (3 X 3 ft) containing food and water and then introducing into the cage a 200-gm albino rat for an additional 2 hours. Only the 24 cats (13 females, 11 males) which did not show any aggression toward the rats were selected for the study. All were maintained on an ad libitum food and water schedule from the time they arrived in the laboratory.

Each of these 24 cats was fitted under aseptic conditions with 10–12 electrode guides mounted over holes drilled in the skull at appropriate stereotaxic coordinates for the implantation of electrodes into the preoptic region, lateral hypothalamus, and

ventral tegmental area of the midbrain. The coordinates according to the atlas of Jasper and Ajmone Marsan [1954] were as follows: midbrain Ant 5.0–7.0 Lat 2.3 hypothalamus Ant 10.0–12.0 Lat 2.5 preoptic region Ant 14.0–16.0 Lat 2.0 and Ant 18.0 Lat 4.0. The electrode guides consisted of 10-mm pieces of 18 gauge wax filled polyethylene tubing. A wire which was attached to several stainless steel screws embedded in the skull served as the reference electrode. The monopolar stimulation electrodes were made from 24-gauge stainless steel rods etched to sharp points in an electrolytic bath of hydrochloric acid and insulated with 3 coats of baked priming paint. The tips were beveled for 160 μ m and the maximum outside diameter of the shafts was 400 μ m. The stimulation consisted of biphasic square wave pulses of 1 msec half cycle duration repeated at a frequency of 60 Hz with the current flow through the cat's brain measured on an oscilloscope.

After each cat had recovered from surgery (4–7 days) it was placed in the test cage with a deeply anesthetized rat and a bowl of food. A sterile calibrated monopolar electrode was then advanced in approximately 0.25–0.50 mm steps through one of the foramina into the preoptic region, hypothalamus or midbrain of the cat. Stimulation was continued at each step and the animal's behavior was noted. Stimulation currents in the range of 100–1,500 μ A were employed during this procedure; the choice of current being dependent on both the vigor and kind of behavior elicited. For example, if stimulation seemed aversive and the cat attempted to escape from the cage, the current was decreased, or if no behavior was elicited, the current was raised until behavioral changes were observed or until 1,500 μ A was reached. In this way the behavioral potential of each site stimulated, as the electrode was lowered, was determined with respect to the test environment. When stimulation elicited a direct approach to the rat and a persistent biting attack on the rat, the electrode was cemented into place and the procedure was repeated until each guide had been implanted with an electrode. If an electrode was advanced to the base of the brain and attack had not been elicited, the electrode was removed and the guide sealed with bone wax to prevent infection. During the first three days which immediately followed the electrode implantations, the peak to peak threshold intensity required to elicit a biting attack on the rat with a frequency of less than 15 seconds was determined for the attack sites. This was done at each site by initially stimulating at an intensity that elicited attack within 15 seconds and then descending in 50 μ A intervals to an intensity at which attack was elicited within 15 seconds on two consecutive trials. The intensity was then raised in 50 μ A and additional trials run. If attack was elicited within 15 seconds for five of six trials, this intensity was taken as the attack threshold. If not, the intensity was raised in 50 μ A steps until the above criterion had been reached. The reliability of the threshold was verified by testing the electrode at the attack threshold intensity to determine if attack within 15 seconds for five of six trials on each of 3 additional

days. If the attack threshold proved unreliable, a new threshold was determined. Individual stimulation trials lasted no more than 20 seconds and at least five minutes between trials.

Testing of points continued for up to six weeks following the determination of the attack threshold intensities. During this time eight cats with attack sites in the preoptic region, lateral hypothalamus, and/or the midbrain ventral tegmental area underwent additional behavioral testing in order to compare the attack behavior elicited during stimulation of each area. The cats selected were those that had attack sites with the most stable thresholds.

Attack object preferences were tested by stimulating the cats with no object in the test cage and with the following objects in the test cage: rat only (R), rat-size wood or styrofoam block (B), food and water (FW), all objects (R/B/FW), rat paired with wood or styrofoam block (R/B), rat paired with food and water (R/FW). As there were seven conditions, these tests were run in blocks of seven trials each, with the order of conditions within each block of trials randomized. Individual trials lasted no more than 20 seconds with at least five minutes between trials. Twelve sites in each area (preoptic region, hypothalamus, midbrain) were tested under these conditions at their attack threshold intensities. An attack site in one region was stimulated for each block of trials, but the order of sites tested for a cat was randomized between blocks. Only one block of trials was run for a single site each day, with six blocks of trials at each site overall. Thus, there were 72 trials for each condition with attack stimulation in the preoptic region, in the hypothalamus, and in the midbrain. Following completion of this testing, the cats had an additional block of six trials of attack stimulation at each site: a) while blindfolded, with the rat in the test cage, to determine if during such stimulation the cats could find and attack the rats without visual guidance; b) in an eight foot long cage to determine if they would approach and attack a rat fed that distance.

After the completion of this testing, the steepness of the attack threshold was estimated for six sites in each region. This was done by determining at each site the maximum intensity at which 15 seconds of stimulation never elicited attack upon the rat (0 of 8 trials) and the lowest intensity at which stimulation always elicited attack upon the rat (8 of 8 trials). Testing began at the attack threshold and continued in steps of less than 500 μA in 10 μA intervals above and below the attack threshold until the criterion of an attack in less than 15 seconds on eight of eight trials was met. If the attack threshold was between 500–1000 μA , the testing was done in 20 μA intervals; if over 1000 μA , in 50 μA intervals. To determine the no attack threshold, the intensity descended until an intensity was found at which stimulation failed to elicit attack in 15 seconds on eight trials. Individual trials never exceeded 20 seconds with at least five minutes between trials. No more than four trials were run at a given intensity at one site on any day with no more than 20 trials at the same site on any day.

At the completion of testing, each cat was anesthetized and perfused with physiological saline followed by 10% formalin. The brains were removed, embedded in

celloidin sectioned and stained with hemotoxylin and eosin. The location of all electrode tips was determined by microscopic examination of the brain sections.

RESULTS

Behavioral

Stimulation of 19 preoptic region sites, 36 lateral hypothalamic sites, and 30 ventral tegmental area sites elicited quiet biting attack behaviors which were seemingly identical in form (i.e. crouched posture, stalking like movements, biting directed to the head and neck of the rat, and lack of observable autonomic effects other than pupillary dilation and mild piloerection). In addition to the topographical similarities, the predatory behaviors elicited by stimulation of the three regions were nearly the same with respect to the preference for the rat as an attack object, the maximum tested distance at which the cat would approach and attack the rat, and the cat's behavior when blindfolded. As is seen in Table I, regardless of the region stimulated, if the rat was in the

TABLE I. A Comparison of the Biting Attack Elicited by Stimulation in the Preoptic Region, Lateral Hypothalamus, and Ventral Tegmental Area of the Midbrain.

Region Stimulated	Condition							
	R	R/B	R/FW	R/B/FW	R Bld	R 8 ft	FW	B
Preoptic area	66	62	64	64	48	52*	26 ^a	23 ^a
Lateral hypothalamus	69	70	65	68	51*	61	7	5
Ventral tegmental area of midbrain	70	69	67	69	41*	53*	2	0

The number of trials out of a total of 72 in which the rat was bitten within 15 seconds of the onset of stimulation is indicated for the following conditions: ■ only rat in test cage; R/B rat and rat-size wood or styrofoam block in test cage; R/FW rat and food and water in test cage; R/B/FW rat, rat-size wood or styrofoam block and food and water in test cage; Bld only rat in test cage but cat blindfolded; R 8 ft only rat but in special 8 ft long test cage. The number of trials (72 maximum) in which only food and water was in the test cage and the food or the food and water containers were bitten within 15 seconds of the onset of stimulation is indicated for the condition FW. The number of trials (72 maximum) in which only a rat-size wood or styrofoam block was in the test cage and it was bitten within 5 seconds of the onset of stimulation is indicated for the condition B. *Significantly different ($P < 0.001$, chi-sq test) from stimulation of other regions in the same condition.

($P < 0.001$)

($P < 0.01$) Significantly different (chi-sq test) from stimulation of same region in condition R.

($P < 0.05$)

There were no significant differences (chi-sq test) in the frequency of attack between regions, neither the ■ Bld or R-8 ft conditions.

cage the cats showed no consistent tendency to attack inanimate objects such as a size wood or styrofoam block food and water containers the cage walls or floors. However with preoptic region stimulation (seven electrodes) and to a lesser extent with lateral hypothalamic stimulation (two electrodes) the cats would bite intermittently at the wood block or food and food and water containers if the rat was not in the test cage. In this regard it needs to be mentioned that a general feature of the implantation of the preoptic region with movable electrodes was the frequent tendency in short fragments of behavior. Many times as electrodes were lowered through the preoptic region biting of the rat was elicited but only if the rat was within a few inches of the cat. When the rat was moved several feet away the stimulated cat failed to approach the rat but would instead bite at the wire mesh floor or food dish if it was nearby. So sites were not considered to be reliable predatory attack sites and with further lowering of these electrodes even these fragments of coordinated attack dropped out. For other implanted electrodes approach and licking of the rat and in the absence of the rat licking of the cage floor and grooming was elicited. While such behavior was occasionally elicited during implantation of the lateral hypothalamus and midbrain ventral tegmental area it was certainly not a general feature. It is also seen in Table I that either placing the rat eight feet from the cat or blindfolding the cat significantly reduced (chi square tests) the number of trials on which the rat was attacked within 15 seconds. However this reduction in frequency of attack was observed for stimulation in each region and there were no significant differences (chi square tests) in the extent of the reduction between regions.

One feature which uniquely characterized the stimulation in each region was the attack threshold. These are shown in Figure 1. It can be seen that the mean threshold for the elicitation of predatory attack with ventral tegmental area stimulation was 310 μ A. In contrast an average of 465 μ A of current was required with lateral hypothalamic stimulation and nearly three times the ventral tegmental area current 840 μ A was required to elicit attack with preoptic region stimulation. It is also seen in Figure 1 that the regional changes in attack threshold were abrupt rather than gradual. In Figure 1 this is most apparent for stimulation in the lateral hypothalamus and the preoptic region. Thus it can be seen that attack thresholds within the lateral hypothalamus (Ant 10 0–12 0) and preoptic region (Ant 14 0–16 0) were stable whereas an 80% increase in the intensity of stimulation required to elicit attack occurred within the two mm of tissue between the lateral hypothalamus (Ant 12 0) and the preoptic region (Ant 14 0). Although it is not shown in this figure previous research indicates that the change in attack threshold while smaller (40%) between the midbrain and hypothalamus may be even more abrupt occurring within the 1 mm of hypothalamic tissue between Ant 9 0 and Ant 10 0 [Bandler 1977]. Table II provides information about the range of attack threshold values in each region. Another feature which was different in each region was the ease of finding sites from which predatory attack could be elicited. Using the identical movable electrode implantation procedure 65% (36 of 55) of the electrodes implanted in the lateral hypothalamus yielded attack. In contrast 43%

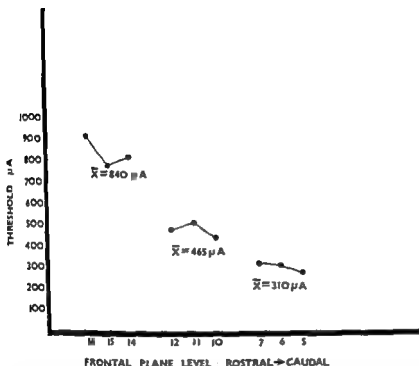


Fig 1 The average threshold intensity for eliciting predatory attack by electrical stimulation is indicated for groups of electrodes implanted at frontal planes from Ant 5.0 to Ant 16.0. The data are from 24 cats and 85 electrodes. Each point represents the average attack threshold intensity for at least five electrodes at each frontal plane level. Differences between average attack threshold intensities for the three regions: midbrain ventral tegmental area (Ant 5.0–Ant 7.0), lateral hypothalamus (Ant 10.0–Ant 12.0) and preoptic region (Ant 14.0–Ant 16.0) were significant ($P < 0.1$, t tests). Attack threshold intensities in microamperes (peak to peak) are represented on the ordinate. Frontal plane levels from Ant 5.0 to Ant 16.0 according to the atlas of Jasper and Ajmone Marchina [1954] are represented on the abscissa.

(30 of 66) ventral tegmental area electrodes and only 25% (19 of 78) preoptic area electrodes elicited attack. Thus preoptic area figure may be low in part because of the tendency for such stimulation to elicit seizures. Thus was the case for an additional six electrodes which initially elicited attack but had to be discarded from the study as repeated stimulation produced limbic type seizures (salivation, twitching of facial muscles, etc.). Including these electrodes would raise the preoptic region yield to 30% (25 of 84 electrodes), still far below the 65% yield in the anatomically adjacent lateral hypothalamus. The lateral hypothalamic and ventral tegmental area figures are in accord with those previously reported [Proshansky and Bandler, 1975 and Bandler, 1977]. Finally, there were also regional differences in the steepness of the

TABLE II Steepness of Attack Threshold in Midbrain Ventral Tegmental Area, Hypothalamus and Preoptic Region

Site	Cat	No attack	100% attack	% Change
Ventral Tegmental Area				
6 OR	12036	240 μ A	320 μ A	33%
6 OL	12036	180 μ A	250 μ A	39%
6 OL	15027	200 μ A	240 μ A	20%
7 OR	17027	280 μ A	340 μ A	21%
8 OR	11306	300 μ A	400 μ A	33%
8 OL	12036	680 μ A	760 μ A	12%
Mean =		315 μ A	385 μ A	26%
Hypothalamus				
10 OR	10086	290 μ A	440 μ A	52%
10 OR	12036	360 μ A	520 μ A	44%
11 OR	10086	310 μ A	400 μ A	29%
12 OL	11256	210 μ A	360 μ A	71%
12 OR	01197	280 μ A	380 μ A	36%
12 OL	15027	520 μ A	700 μ A	35%
Mean =		330 μ A	465 μ A	44%
Preoptic Region				
14 OR (a)	01197	800 μ A	1200 μ A	50%
14 OR (b)	01197	560 μ A	800 μ A	45%
14 OR	20097A	600 μ A	840 μ A	40%
14 OL	20097B	580 μ A	800 μ A	38%
15 OR	17027	620 μ A	780 μ A	26%
16 OL	20097B	640 μ A	960 μ A	50%
Mean =		630 μ A	895 μ A	42%

attack thresholds. It can be seen in Table II that for attack sites in the ventral tegmental area and lateral hypothalamus there was no significant difference in the maximum stimulation intensity (315 vs 330 μ A) at which attack was never elicited. However, whereas a 26% increase in this intensity elicited a 100% reliable attack for ventral tegmental area stimulation, a 44% increase in stimulation intensity was required before this level of reliability was achieved with lateral hypothalamic stimulation (this difference was significant $P < 0.05$ t test). For preoptic region sites the maximum intensity at which attack was never elicited was significantly higher than that in the ventral tegmental area or lateral hypothalamus (630 μ A vs 315 μ A and 330 μ A). However, the mean increase in intensity required to elicit 100% reliable attack was nearly identical to that required with lateral hypothalamic stimulation (42% vs 44%).

histological

Electrode tip locations of attack sites in the lateral hypothalamus and ventral tegmental area have been described in great detail in previous reports [Bandler et al. 1972; Goshansky and Bandtke 1975; Flynn 1972] and will not be shown here. Electrode tip location for the preoptic region attack sites are shown in Figure 2. It is seen that attack is elicited from a very widespread area especially within the caudal preoptic region. Support of this conclusion is the observation that for three cats attack was elicited from comparable intensities from pairs of electrodes which were implanted at approximately the same coronal plane (Ant 14.0) but at both 2.0 mm and 4.0 mm lateral to the midline per se. Within the lateral hypothalamus and ventral tegmental area electrodes implanted only within a much narrower (approximately 0.5–1.00 mm) medial lateral zone elicit predatory behavior.

These histological findings are seemingly in sharp contrast to the earlier report of Inselman and Flynn [1972] that attack behavior is elicited only from the medial preoptic area and the more medial portions of the lateral preoptic area. One difference in the two studies is that from their histology it appears Inselman and Flynn implanted only 29 electrodes in the preoptic region in contrast to the 84 (including the seizure eliciting electrodes) electrodes of this study. More importantly they implanted no

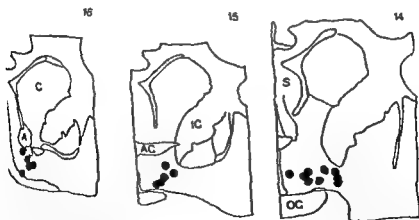


Fig. 2. Map of preoptic points from which predatory attack was elicited by electrical stimulation in the cat. Electrode tip locations indicated by solid circles. Sections are drawn according to the atlas of Jasper and Ajmonia Marsan [1954]. Anterior frontal plane for each section is in the upper right corner. Abbreviations: A, accumbens nucleus; AC, anterior commissure; IC, internal capsule; OC, optic chiasm; S, septum.

electrodes in the lateral portions of the caudal lateral preoptic region (Ant 13.5-14.5). This caudal lateral preoptic region is precisely the area in which five of our 19 attack electrodes were located (see Fig. 2). Inselman and Flynn's conclusion then is based on their inadvertent failure to explore this region. Within the more rostral reaches of the preoptic region (Ant 15.0-16.0) we found that eight of 10 attack electrodes were either in the medial preoptic region or the medial portions of the lateral preoptic region and this is in substantial agreement with Inselman and Flynn [1972]. A second factor that may have contributed to the differences in the two studies is that Inselman and Flynn [1972] used a maximum stimulation intensity of 800 μ A. Of the 19 preoptic attack-eliciting electrodes in this study, only 10 electrodes elicited reliable attack at intensities of 800 μ A or less, although it should be noted that three of these were in the lateral portions of the lateral preoptic region. The different results of the two studies then are seemingly reconcilable. Within the rostral reaches of the preoptic region attack is elicited from the medial preoptic area and the medial portions of the lateral preoptic area, whereas in those portions of the preoptic region contiguous with the anterior hypothalamus predatory-like attack is elicited from a widespread region extending from the medial to the far lateral preoptic region. It may be noted that the first mention of biting attack elicited by preoptic region stimulation includes a site in this far lateral caudal preoptic region [Hutchinson and Renfrew, 1966].

DISCUSSION

It is well established that the ascending and descending components of the medial brain bundle are most compactly arranged within the ventral tegmental area of the brain and that they come to occupy increasingly large cross sectional areas in successive lateral hypothalamic and preoptic region levels. That the medial forebrain bundle provides the common neuropil which would be affected by stimulation in each region likely explains the similarity in the form and selectivity of the elicited predatory behaviors. The differing regional anatomy may well explain many of the regional differences.

With respect to the lateral hypothalamus and ventral tegmental area, the attack threshold intensity differences, the differences in the steepness of the attack threshold and the differing probabilities of eliciting attack behavior with implanted electrodes are all in accord with the medial forebrain bundle anatomy. Thus, because of the greater compactness of the medial forebrain bundle within the ventral tegmental area, we expect that it should be harder (than it would be in the lateral hypothalamus) to implant electrodes in the proper spot, but when so placed, lower intensities of stimulation should affect a greater proportion of the medial forebrain bundle, yielding a greater proportion of lower attack thresholds. Other factors, however, may be involved as well. For example, within the midbrain, moderate intensities of stimulation elicit more dramatic converging motor responses than in the lateral hypothalamus. Such responses could certainly

under the discovery of other ventral midbrain sites that might only elicit attack at high stimulation intensities. Still the greater steepness of the attack threshold in the ventral tegmental area cannot be explained by competing responses. Further in a recent study [Bandler and Fatounis 1976] we found that prior (priming) stimulation of attack sites in the ventral tegmental area was more effective in altering the subsequent excitability (reducing attack latencies) of stimulation at lateral hypothalamic sites than prior stimulation at adjacent lateral hypothalamic sites. This suggested that there is a greater correspondence between the neuropil affected by stimulation of a ventral tegmental area attack site and a lateral hypothalamic attack site than there was between sites affected by two lateral hypothalamic sites. Such results are in accord with assigning the greater compactness of the medial forebrain bundle in the midbrain ventral tegmental area a major role in explaining differences in the effects of stimulation in these two regions.

Exactly the reverse explanation—the diffuseness of the medial forebrain bundle in the preoptic region—may offer a partial explanation of the preoptic region results but is perhaps because of the diffuseness of the medial forebrain bundle within the preoptic region only with very high intensity stimulation is enough of the attack relevant neuropil affected to elicit a biting attack on the rat. In this regard it should be recalled that in the absence of the rat stimulation of some preoptic attack sites evoked biting at inanimate objects and in addition that a general feature of implantation of the preoptic region with movable electrodes was the tendency to elicit fragments of behavior. It has previously been suggested that the neural pathways mediating the approach to the rat and the biting of the rat are anatomically separable [Proshansky and Bandler 1975]. In this context both the fragmentation of behavior observed during electrode implantation in the preoptic region and the tendency for preoptic region attack stimulation to elicit generalized biting in the absence of the rat may indicate an anatomical separation of functionally relevant components (i.e. biting in one vs. approach in the other) within the medial forebrain bundle in the preoptic region. In summary we are speculating that because the medial forebrain bundle is relatively compact in the lateral hypothalamus and midbrain ventral tegmental area stimulation in these regions usually elicits complete attack sequences (i.e. approach and biting), whereas in the preoptic region because the medial forebrain bundle is more diffuse stimulation is more likely to not elicit attack or to elicit only components of the attack sequence (i.e. approach or biting). There may as well be other factors such as a unique regional synaptic physiology that contribute to the increased probability of fragmented behavior in the preoptic region.

It has previously been reported that large anterior hypothalamic lesions do not affect the predatory behavior elicited by stimulation of the caudal lateral hypothalamus [Bergquist 1970]. On the other hand small ventral tegmental area lesions [Proshansky et al. 1974, Proshansky and Bandler 1975] or large midbrain reticular formation lesions [Berntson 1972] eliminate the attack elicited by lateral hypothalamic stimulation. We had thought [Proshansky and Bandler 1975] as have others

[Bergquist 1970 Berntson 1972 Chi et al 1976 Flynn 1976] that the different effectiveness of these lesions indicated that the hypothalamus and midbrain stimulation elicited attack behavior because of the effects of the stimulation on descending neural pathways. While this interpretation may yet prove to be substantially correct, the data of this study are also consistent with another interpretation, namely that the posterior hypothalamic and midbrain lesions may be effective not because of the directionality of the stimulation effects but simply because of the greater compactness of the medial forebrain bundle in the posterior lateral hypothalamus ventral midbrain tegmental region. Thus, even large anterior hypothalamic preoptic region lesions may be ineffective because they are less likely to destroy neuropil in common with other lateral hypothalamic attack sites than are small midbrain ventral tegmental area lesions.

When lesions are made in two different regions such as the anterior hypothalamic preoptic region and the ventral tegmental area, and we suspect that there are large differences in the configuration of the neuropil affected by the lesions, the interpretation of results is difficult. For this reason, any conclusions about the directionality of stimulation effects would seem to be premature.

In a recent study, Berntson et al [1976] drew attention to the extent to which the predatory behavior elicited by stimulation resembled natural predatory behavior if the cats were tested with live rats in a naturalistic environment. For example, in such an environment, stimulated cats used their paws to drive a live rat from behind an obstacle which made it impossible for the cat to bite the rat. Such complex behavior would likely depend upon forebrain rather than brainstem mechanisms. In a review article, Siegel and Edinger [1978] have gone further and suggested that in the intact cat, the neocortex is likely involved in the organization and character of the centrally-elicited attack behavior. Modifying Flynn's [1972] terminology, they proposed the term "cortical patterning mechanism" and suggested that the brain stimulation that elicits attack must ultimately produce altered patterns of neural activity in parietal, temporal, and frontal neocortices.

If this proves to be substantially correct, the results of this study suggest that electrical stimulation of the preoptic region, lateral hypothalamus, and midbrain ventral tegmental area may well alter forebrain neural activity via effects on components of the ascending medial forebrain bundle. However, ascending pathways other than those within the medial forebrain bundle would likely be involved in mediating the effects of attack stimulation in other regions, as it should be recalled that Ellison and Fernald [1968] have reported that midbrain reticular formation stimulation (not to be confused with midbrain ventral tegmental area stimulation) elicits attack after surgical isolation of the hypothalamus.

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Factors in the Waning of Muricide in the Rat II Digging Behavior

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If each mouse killed by a rat is removed from the rat's home cage and replaced immediately by another, the decline in the rate of killing within the one-hour sessions is accompanied by an increase in digging in the woodchip bedding material. Deprivation of the opportunity to dig by removal of the bedding material results in a statistically significant increase in kill rate. Since no other behaviors monitored showed a similar increase with this manipulation, it appears that digging may be a mechanism important in the waning of muricide. Furthermore, digging may be, in some sense, a functional equivalent of killing.

Key words: muricide, habituation, displacement, digging.

In an earlier study [Potegal, Marotta, and Gimino, 1975] we found that the characteristics of the intrasession waning of muricide were not those of habituation, at least as defined by Groves and Thompson [1970]. In searching for alternative mechanisms underlying this intrasession decrement, we noted a marked increase in a form of forward-directed digging which accompanied the decreases in muricidal behavior. Although digging may occur in other situations, e.g., immediately after the bedding material (woodchips) has been changed, it seemed possible that the increase in digging during the session might play a role in the waning of muricide.

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Digging particularly in agonistic situations has been described as a displacement behavior in various species of rodents including the prairie dog [Smith Smith Oppenheimer deVila and Ulmer, 1973] vole [Clarke 1956] multimar mate mouse [Veenstra 1958] and rat [Barnett 1958 Grant 1963]. Although the notion of displacement behaviors has been quite controversial in part because of its association with the now discredited 'energy conservation' theories of motivation [Hinde 1970] recent evidence [Wilz 1975] has shown that the occurrence of such behaviors may indeed have a functional role in modifying an organism's subsequent aggressive behavior.

In the current context it is conceivable that the occurrence of forward digging may influence the probability of subsequent killing. Delius' hypothesis [1967] that displacement behavior may act as a de-arousal mechanism implies that the occurrence of displacement digging could reduce muricide rates. Similarly Heiligenberg [1965] noted that some species of cichlids increase digs at the substrate under certain conditions in which their attack readiness had also increased. He argued that the failure of attack rates to rise after a bout of digging indicates that the digging counteracted the spontaneous increase in attack rate that routinely occurred during these particular conditions. These observations could be encompassed in a satiation model of muricide in which digging was a motivational equivalent of killing. In these circumstances it could be predicted that deprivation of the opportunity to dig would tend to increase kill rates.

Alternatively, digging could conceivably facilitate killing. post kill digging might act as a warm up for the next kill. In a study of agonistic encounters in jungle fowl, Feehes [1972] found that pecking at the ground, opportunistically directed toward particles of sand on the floor, was positively correlated with occurrence of an agonistic side display posture. When the sand was removed and ground pecking consequently eliminated, the incidence of aggressive pecking and kicking at conspecifics was also reduced in these encounters. This is the only study of aggressive behavior known to us in which the opportunity to perform displacement behaviors has been manipulated.

We decided to put these alternative hypotheses about killing and digging to the test by comparing the kill rates of muricidal rats with or without the opportunity to dig.

METHOD

Subjects. Our subjects were male Long Evans hooded rats, 6-12 months old, which had killed the first mouse put into their home cage within 5 minutes. Five of these animals (the prior experience group) had killed a mean of 165 mice (10 mice/session, approximately) in our previous experiments on inter-session interval effects [Potegal et al 1975, Exp 2]. We compared the behavior of these subjects with that of 6 additional naive rats selected by the same criterion from the same

sto k (no prior experience group) However we rejected any rat that killed more than 25 mice in any of the first 3 sessions. Subjects were singly housed and maintained in large plastic home cages as described in our previous report. The cages were routinely filled with Sani-chip bedding material (Animal Feeds Bronx New York) to a depth of 2.5 cm. The bedding material was changed twice weekly on sessions in which no behavioral testing was done.

Procedure All subjects were tested for 20 one hour sessions in their home cages with or without the woodchip bedding material in a repeated ABBA order. In the woodchip-absent condition the woodchips were removed 12 hours before testing. The intersession interval was at least 48 hours. A session began when a mouse grasped with forceps was presented into a corner of the cage not visible to the rat. When the mouse was killed it was immediately removed and replaced by a new one hence a live mouse was almost continuously present during the session. A continuous record of killing digging grooming feeding was made by the experimenter with a 20-pen event recorder. In addition any nipping rough grooming or sudden strikes toward the mouse were recorded as attack.

RESULTS

Overall Relationship of Muricide and Digging

Figure 1 illustrates the average time courses of killing and forward digging throughout all woodchip present sessions. Note that digging increased at the beginning

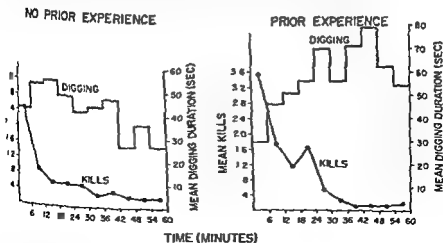


Fig. 1. Mean intrasession distribution of number of kills and duration of digging in successive minute periods.

of the session as the first burst of killing waned. Digging then started to decline toward the end of the session. These effects were more pronounced in the experienced group. This group also showed a transient increase in muncide in 18–24th minute period followed by a surge of digging in the next 6 minutes. These peaks also appeared in separate analyses of the first 10 and last 10 sessions indicating that they were a stable feature of muncide in this group. The occurrence of such successive peaks was also detected, with a somewhat different analysis in our earlier study [Potegal et al. 1975].

Results of Woodchip Removal

The removal of the woodchips substantially reduced, but did not entirely eliminate, forward digging since eight of the subjects occasionally dug at food pellets, feces, or even the bare cage bottoms. This appears to be an *in vacuo* digging response [Lorenz, 1957]. In conjunction with these *in vacuo* digging attempts, we have seen two of the rats pick up food pellets or feces in their mouths and drop them on or near the mouse. Since digging is often directed towards the mouse, and occasionally results in the mouse being covered by a mound of woodchips [Potegal et al. 1975; cf. Pinel and Treit, 1978], this behavior may be an interesting case of response equivalence. Similar observations have been made in prairie dogs [Smith et al. 1973].

Overall, nine of the 11 subjects killed more mice when the woodchips were absent (Wilcoxon signed rank, matched pairs test, $T=9$, $P<0.05$). The mean numbers of mice killed per session in the first 10 and last 10 sessions in both conditions are shown in Table I. Two findings suggest that the relationship between digging and killing may have become stronger with experience. Firstly, Wilcoxon tests of differences between all sessions with or without woodchips for individual subjects showed significant kill rate differences between conditions for each of the 5 subjects with prior muncide experience ($P<0.001$ for each). None of the six rats without prior experience had statistically significant individual inter-

TABLE I Mean Number of Kills/Session

	N	Sessions 1–10		Sessions 11–20	
		Woodchips	No woodchips	Woodchips	No woodchips
No prior experience	6	7.2	7.3	6.5	8.8
Prior experience	5	9.6	12.9	6.4	11.0

condition differences. Secondly, over all subjects, differences between conditions in sessions 1-10 were not significant while inter-condition differences in sessions 11-20 were significant ($T=4$, $P<0.01$). There were no differences between conditions in any of the other behaviors monitored, including attack. There were no differences in duration of digging in woodchips between first 10 and last 10 sessions.

To test the hypothesis that the increase of killing in the absence of woodchips affected the absolute or relative prepotency of killing in our standard woodchips present condition, we calculated the percentage increase in killing between conditions for each subject. Spearman rank order correlations across all subjects were made between 1) the percentage increases and kill rates and 2) the percentage increases and kill rate/grooming duration ratios. No significant correlations were found between the absolute or the relative (to grooming) amount of killing in the woodchip condition and the percentage increase between conditions.

DISCUSSION

Temporal Relationship Between Killing and Digging

Over the whole session, killing and forward digging tended to be reciprocally related. Within certain portions of the session, peaks in killing were followed by peaks in digging. Other studies have also turned up a diversity of temporal relationships between aggressive behavior and displacement activity. Gallagher, Herz, and Peeke [1972] found that picks at the bottom of the aquarium were positively related with bites directed at a neighboring conspecific in convict cichlids. However, Peeke and Peeke [1972] reported that bottom pick frequency was inversely related to frequency of predatory attack by goldfish on brine shrimp. In correlational studies on several species of cichlids, Heiligenberg [1965] and Rasa [1971] included that the occurrence of "digging" or "chasing" reduces subsequent aggression. Interestingly, Rasa [1971, p. 48] reports that "On every occasion a peak in aggressive motivation is elicited; this is followed within the next five minutes by one in chasing." As in our study, Rasa's results showed that displacement activity and overt attack were sometimes directly and sometimes reciprocally related. Our study further suggests that these relationships can be strengthened with experience. We know of no other demonstrations of this kind.

Effects of Deprivation of Digging

Depriving rats of the opportunity to dig significantly increased mouse killing at least in rats selected for low initial rates of killing. These results contrast with those of Feekes [1972] who found decreases in conspecific attack following deprivation of ground pecking in junglefowl. Difference in species, experimental situations, and motivational systems clearly render comparisons problematic.

Several possible explanations exist for our effects. One of the most obvious interpretations is the response competition hypothesis, with the time formerly

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Visual Target Control of Schedule-Induced Aggression in White King Pigeons (*Columba livia*)

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Visual target control of schedule-induced attack was studied in domesticated pigeons by exposing them to successive and simultaneous target preference procedures involving a fixed time food schedule and projected target images. Pigeons preferred attacking an image of a conspecific head over a headless bird regardless of the height of the latter. Images of an intact bird and of a head alone were equally effective in controlling attack and more effective than the headless bird. Neither the eye nor four other head-related features exclusively controlled attack. The combined results suggest that the head of an intact conspecific target selectively controls schedule-induced attack and that the effectiveness of the head in directing attack is inversely related to its physical integrity as a unit without regard to specific features. These results are consistent with reports that the head and head-related features of an intruder control reproductive aggression in birds.

Key words: aggression, schedule-induced, pigeon, conspecific target preference, visual features

DISCUSSION

Schedule-induced shock-elicited and other types of irritable aggression (Cohen & Yoburn, 1976) are directed toward a variety of targets including conspecifics, inanimate objects, and inanimate objects. Experiments that have used a conspecific target for studying irritable aggression typically find that gross changes in its be-

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havioral and physical properties can significantly influence aggressive behavior (eg Azrin Hutchinson and Hake 1966 Powell Francis Braman and Schneiderman 1969 Hynan 1976 Cohen and Looney 1973 Knutsen 1973) Looney and Cohen [1974] reported that a global change in just the visual aspects of a conspecific target affect schedule induced aggression in pigeons. They found that an image of a conspecific silhouette is more effective in controlling aggression than a comparable inverted silhouette outline of a conspecific or colored paper. The present experiments assess the specificity of visual target control of schedule induced aggression in domesticated pigeons. In particular, the experiments determine if the head of a colored conspecific target image which is the locus of contact [Looney and Cohen 1974] selectively controls schedule induced attack. Such selective visual control would be consistent with the results of studies on reproductive aggression in birds [eg Smith and Hoskings 1955 Stout and Brass 1969].

GENERAL METHOD

Subjects and Apparatus

Seventeen male domesticated White King pigeons (from Palmetto Pigeon Plant Sumter South Carolina) were maintained at 75% (± 20 gm) of their free feeding weights. Supplemental feedings of mixed grain following test sessions were given when necessary. Birds were visually isolated in individual home cages with free access to water and health grit under a 16/8 hour light/dark cycle.

Pigeons were tested six days/week in a 34.9-cm X 74.9-cm X 70.8-cm test chamber. A 5.0-cm X 5.7-cm opening (9.5 cm above the floor) centered on one chamber wall allowed subjects access to mixed grain when the food hopper (BRS/LVE 114-10) was raised. A photocell was mounted below the food tray opposite the hopper light so as to accurately time each eating bout from its onset. Centered on the wall opposite the hopper were two 12.5-cm X 16.5-cm Polycarbonate plastic screens spaced 8.5 cm apart center-to-center. Each screen was suspended by two frame mounted micro-switches (Micro Switch No 311SM701T) centered behind an 11.5-cm X 15.3-cm opening in the black rear wall. The bottom edge of the screens was 7.6 cm above the chamber floor. An attack was defined as displacement of any point on either screen with a force of approximately 0.1 N (measured by a Jonard dynamometer). In order to prevent damage to the screen and eliminate reflections, each screen was covered with a piece of seamless Scotch Brand Mending Tape.

Targets

Located directly behind each screen was a random access projector [Cohen Yoburn and Looney 1976] which displayed on that screen colored conspecific or degraded conspecific images (Figs 1 and 2) on an illuminated background. An



Headless

Raised
Headless

Intact

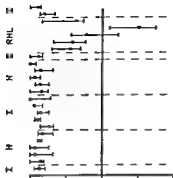
Fig. 1. Black and white photographs of the rear view projected colored con-
sistent targets used in Experiments 1, 2, and 3.

A blank background alone (blank target) was used in conjunction with images in Experiments 2 and 3. The image of the intact conspecific was 15.3 cm high, the head located at approximately the subject's head height. The distance from the center of the eye to the tip of the beak was 3.8 cm, which is approximately that of a live White King pigeon. The size of the head and headless images was the same as those features of the intact image. In addition, all degraded images except the raised headless were positioned on the screen in the same place as the intact image. As shown in Figure 1, the raised headless image was placed to the upper edge of the screen. During sessions in which the projectors were used, they provided the only light source in the chamber, approximately 1.37 mcd/m² each. During all other sessions, the rear chamber wall was replaced with a smooth black surface and chamber illumination was provided by two 6.3 W 16-W lights located in the ceiling in front of the food hopper panel. Timing and recording of experimental events was controlled by relays, timers, and counters located in a room adjacent to the chamber. White noise and an exhaust fan served to partially mask extraneous sounds.

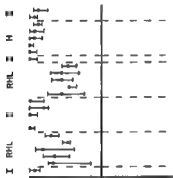
Preference Procedure

During testing, all animals were exposed to a fixed time 90-second schedule of food presentation which permitted limited access to food every 90 seconds independently of the animal's behavior. Each of 30 three second food presentations in a session was timed from the moment of interruption of the hopper photobeam. A session began with a food delivery and ended with 90 seconds without light. A protective contingency was programmed for all experiments such that a scheduled food delivery was delayed until target responding had not occurred for 5 seconds. This arrangement ensured that attacks on the target were not adversely reinforced by food [Azrin and Hutchinson, 1967].

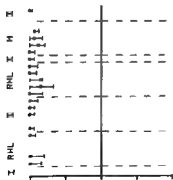
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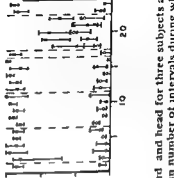
P 7384



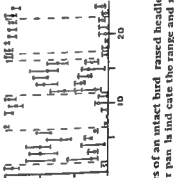
P 8594



P 7928



P 7384



P 8594

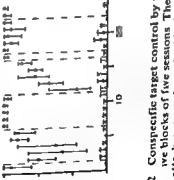


Fig. 2 Conspecific target control by images of an intact bird raised headless bird and head for three subjects across five blocks of five sessions. The lower panel indicates the range and median number of intervals during which a stimulus occurred on the blank target (O) versus the conspecific image (■). The upper panels show the median number of intervals (SD) and range (SE) of +10.0 and -10.0 corresponding to a complete preference for the on pe f.

The target preference procedure involved concurrent exposure to the fixed time and a pair of rear view projected target stimuli. During each target preference session only one pair of stimuli was used and only one stimulus appeared on a screen at a time.

While subjects were feeding the relative position of a pair of stimuli semi-randomly changed between screens such that the location of the stimuli was sometimes different at the end of each feeding bout. Within a session each stimulus appeared on each screen an equal number of times during successive blocks of six food presentations. One of four sequences was repeated every fourth session the position of the two stimuli at the beginning of a session was reversed. The total number of attacks on each screen, cumulative duration (min) of attacks on each screen (switch closure times) recorded in terms of 0.12 second the location of the first attack following each food delivery were recorded only for both stimuli regardless of position.

2.7.1

Although there has been considerable interest in intraspecific aggression in penguins and doves (e.g. Fabricius and Janzson 1963, Orcutt 1971, Vowles and Wood 1966) there is virtually no information about which visual features control target control aggression in Columbidae. Using White King pigeons the first experiment examines target control by conspecific images of a headless bird and intact bird.

2.7.2

This experiment evaluates the pigeon's target preference when given a choice between attacking images of a head and a headless bird.

2.7.2.1. THOD

Three pigeons (P8835, P6222, P7041) with a history of schedule induced attack against a conspecific image [Looney et al. 1976] were exposed to the standard target preference procedure described above with images semi-randomly changing during each food presentation. Initially each bird was given a choice between attacking images of a head and of a headless bird (see Fig. 1) for 6-22 sessions and then between images of a head and of a headless bird raised to head height for 10-20 sessions.

RESULTS AND DISCUSSION

All three birds had stable target preferences across all test sessions when given a choice between attacking an image of a head versus an image of a headless bird in either the normal or head height position. Preferences during the final five

TABLE 1 Target Preferences During Exposure to a Head Versus a Headless Target Image in Either the Normal or Head Height Position*

Pigeon	Initial attack		Head vs headless bird				Total attack duration (min)			
			Total attacks/session							
	Head	Headless	SI	Head	Headless	SI	Head	Headless	SI	SI
8835	29.8	0.2	+0.99	429.2	7.0	+0.97	0.16	0.00		+1.00
6222	24.8	0.0	+1.00	433.2	5.0	+0.97	0.36	0.01		+0.92
7041	27.6	2.4	+0.85	1031.4	68.0	+0.87	2.89	0.15		+0.92
Head vs raised headless bird										
8835	29.2	0.8	+0.95	441.0	12.6	+0.94	0.81	0.03		+0.93
6222	29.4	0.2	+0.99	534.2	1.6	+0.99	1.86	0.00		+1.00
7041	27.8	2.2	+0.86	1105.4	57.6	+0.89	3.24	0.07		+0.96

Means over the last five sessions are presented for location of the initial attack following food (maximum of 30) total attacks/session and total attack duration per session on the head and headless targets. The sensitivity index (SI) computed from these means (last five sessions) is presented for each measure.

sessions of each target condition are summarized in Table 1. A sensitivity index (SI) [Frey and Colliver 1973] was computed for each measure of attack over the last five sessions of each condition. The SI is an index of image preference independent of position preference.

$$SI = \frac{P_1 - P_2}{2(P_1 + P_2) - (P_1 + P_2)^2}$$

where

P_1 = P(attack left|head left)

P_2 = P(attack left|head right)

As computed in this table, sensitivity indices of +1.0, 0.0, and -1.0 correspond to a complete head preference, no preference, and a complete headless bird preference, respectively. The upper portion of Table 1 shows that, with the image of the headless bird in its normal position, all three pigeons showed a strong preference in terms of all three measures for attacking the screen on which the head was projected. Informal observations indicated that these pigeons, like those in previous schedule-induced attack experiments [e.g., Looney and Cohen 1974], charged and pecked directly on the head.

It is possible that the pigeons were not exhibiting a preference for the image of the head but rather a preference for a head-height image over one below head height. However, the results in the bottom part of Table 1 indicated that this was not the case. With the headless image raised to a subject's head height, all three continued to show, by all measures, an extreme preference for attacking the image of the head.

In this experiment, as well as in Experiments 1b-3 described below, the frequency and temporal pattern of attack within a session were comparable to that reported in previous schedule-induced attack studies [Flory 1969; Cohen et al 1976]. Attack occurred following most of the 30 food deliveries (Table 1) with the probability of attack highest following food.

EXPERIMENT 1b

In the previous experiment, pigeons preferred to attack an image of a complete head over a simultaneously presented image of a headless bird. The next phase of the experiment assesses the relative effectiveness of those targets, as well as an intact target image, when only one image is presented at a time. Specifically, Experiment 1b determines if images of the head and intact bird are equally effective in controlling aggression when presented singly and if the extremely low levels of attack on the headless bird in the previous experiment were related to the concurrent availability of the head.

METHOD

Attack was established in four of five experimentally naive pigeons using a procedure developed by Looney et al [1976]. Briefly pigeons were exposed to a fixed time 90 second schedule with ten 10-second food presentations for 75 sessions with no target image present. On the 26th day of exposure to that schedule the image of the intact bird was projected on the right screen and background illumination alone (blank target) was projected on the left screen. After 20-71 sessions with those stimuli present birds that had attack rates of 1.0 response/minute or more were exposed to twenty 20 minute sessions with the same target conditions but no food scheduled and then an additional 10 sessions with the FT schedule reinstated. Finally each bird was exposed to five additional sessions with the FT schedule in effect but with the target stimuli alternating position during each food presentation.

Following this preliminary training birds were exposed to the target preference procedure in which they had a choice between attacking an image of a conspecific (head intact raised headless) or a blank target. P8594 and P7834 were given a choice between attacking a blank target and the conspecific images in the following order with the number in parentheses corresponding to number of sessions: intact (5) raised headless (25) intact (5) raised headless (25) intact (5) head (25) intact (10). P7928 and P7306 were exposed to the same target images in a different sequence: intact (5) head (25) intact (25) head (25) intact (5) raised headless (25) intact (10). As in Experiment 1a targets semi-randomly changed position at each food presentation and a test session consisted of 30 food presentations on the FT 90-s schedule.

RESULTS AND DISCUSSION

For three of the four pigeons that attacked the conspecific image during preliminary training continued exposure to the food schedule was necessary to maintain attack. Removal and reinstatement of the schedule prior to preference testing resulted in at least a two fold decrease and then increase respectively in attack rates for each bird except P7928 for which there was no effect. Long term perseveration of schedule induced attack in the absence of a food schedule was also reported by Looney et al [1976] and on the basis of their results would be expected to decrease with additional exposure to the no-schedule condition.

Figure 2 summarizes the results obtained for P8594, P7384 and P7928 when only one conspecific image (head raised headless or intact bird) and the background illumination (blank target) were presented. The data for the fourth bird (P7306) is not included in this figure since for unknown reasons it stopped attacking all targets following the second exposure to the intact image (session 65). The lower panel plots the median number of inter food intervals in which the

initial attack occurred on each of the three conspecific images (closed squares) and the blank target (open circles) over successive blocks of five sessions. This measure of attack is positively correlated with median attack rate (Pearson Product Moment correlations of +0.82, +0.73 and +0.44 for P7928, P7384 and P8594 respectively) but is more stable from session to session. The data in the lower panel are replotted in the upper one in terms of median sensitivity index (Frey and Collier 1973).

When either the head or intact bird was presented with the blank target, all birds attacked at least once during most inter food intervals (lower panel). In addition, 90% or more of those initial attacks were directed toward the conspecific rather than the blank target which is reflected in sensitivity indices ranging from +0.74 to +1.00 (upper panel). Corresponding data for the fourth bird (P1306) not included in this figure are consistent with that of the other three in that attacks occurred during 80% or more of the inter food intervals with the head or head available and median sensitivity indices ranged between +0.77 and +1.00.

With the image of the raised headless bird present, P8594 showed an extreme preference for it relative to the blank target (median sensitivity indices of +0.93 to +1.00, upper panel). The remaining two birds (P7384, P7928) showed less of a preference for the headless bird (relative to the blank target) than they did for either the head or intact bird. All three pigeons, however, attacked the headless target in fewer inter food intervals than they attacked either the head or intact bird (lower panel). Perhaps the discrepancy between preference for the headless target and probability of attacking it observed for P8594 is most likely to occur with ineffective targets. Such discrepancies also reported by Looney and Hen [1974] may justify distinguishing between the direction and release induced aggression by a conspecific target. The directive property may be assessed in terms of the location of the initial attack on one of two simultaneously available targets following food delivery and the releasing property evaluated in terms of the number of inter food intervals with an attack or latency of attack following food presentation.

Comparable target control by images of the head and intact bird in this experiment indicates that the effectiveness of a conspecific image in sustaining attack is monotonically related to target size (area). The physical size of the least effective target, the headless image, was intermediate to that of the head and intact bird. On the other hand, the fact that the birds reacted in the same way to images of the head and intact bird suggests that a pigeon may selectively attend to the head of a conspecific target when attacking. The partial effectiveness of the headless bird in sustaining attack may have resulted from it sharing features with the head (e.g. white feather surface) or from its prior association with the head.

EXPERIMENT 2

The extreme target preference for the head over a headless bird in Experiment 1a and the comparable target control by the head and intact target images in Experiment 1b suggests that the head of a conspecific image or some aspect(s) of it may selectively control schedule induced aggression. In that case, one would expect that when presented simultaneously, images of an intact bird and head would be equally effective in controlling attack. On the other hand, when confronted with images of an intact bird and headless bird, pigeons should show a consistent preference for the intact bird. The next experiment examines these questions.

METHOD

The same preliminary training procedure employed in Experiment 1b was used to establish attack against an image of the intact bird (Fig. 1) in each of the nine experimentally naive birds.

Following preliminary training, birds were exposed for five sessions to the target preference procedure in which they had a choice between attacking an image of an intact bird or a blank target. Targets randomly changed position during food presentation. Following the fifth session, each subject was exposed to a probe session with three birds arbitrarily assigned to one of three probe testing conditions. The probe session was identical to the previous baseline conditions except that the blank target was replaced by a comparison target, which was either a headless image, raised headless image, or head (Fig. 1).

RESULTS AND DISCUSSION

Removal and reinstatement of the FT schedule prior to preference testing indicated that the food schedule increased the level of attack. For all birds, removal of the schedule resulted in at least a two-fold decrease in attack rate relative to the schedule condition.

Target preferences (total attacks/session) are summarized in Table II for both the final baseline session (intact image and blank screen) and the probe session (intact image and degraded comparison image). P9093, P7329, and P7797 (upper portion) showed an extreme preference for the intact image over the blank target during the final baseline session ($SI = +0.89$ to $+0.99$) but failed to show a strong, consistent preference for either the head or intact image during the probe session ($SI = -0.18$ to $+0.06$). Comparable results (not included in Table II) were obtained from a preliminary study in which the birds previously used in Experiment 1 were exposed to several sessions with access to images of a head and headless conspecific followed by a probe session with images of the intact bird and head available. Although all three pigeons initially showed an extreme preference ($SI = +0.6$

TABLE II Target Preferences During the Final Baseline Session With the Intact Bird and Blank Target Available and the Subsequent Probe Session With the Intact Bird Versus One of Three Degraded Comparison Targets (Head Headless or Raised Headless Bird) Present *

Pigeon	Intact bird	Blank	SI	Intact bird	Head	SI
9993	507	3	+0.99	189	257	-0.18
1379	535	32	+0.89	398	480	-0.07
7197	717	8	+0.96	262	256	+0.06
	Intact bird	Blank	SI	Intact bird	Raised headless	SI
8153	108	3	+0.92	150	8	+0.85
8070	1155	5	+0.99	678	132	+0.69
8346	571	5	+0.98	441	26	+0.89
	Intact bird	Blank	SI	Intact bird	Headless	SI
8181	54	0	+0.74	88	37	+0.55
8108	148	3	+0.96	90	2	+0.95
8172	451	25	+0.90	320	53	+0.72

*The total number of attack /session on the blank and conspecific targets and the corresponding sensitivity index (SI) are included

to +1.00) for the head relative to the headless bird there was not a consistent preference for either the head or intact bird ($SI = -0.44$ to $+0.26$) during the subsequent probe session for any subject.

The results for the six remaining pigeons (lower portion of Table II) suggest that the lack of differential target control by the intact bird relative to the head is due to selective target control by the head of the intact target. All six birds exhibited a preference for the intact image relative to the blank target during the final baseline session ($SI = +0.74$ to $+0.99$) and continued to have a preference which was slightly attenuated for the intact image over a raised or lowered headless target during the probe session ($SI = +0.55$ to $+0.95$). This preference for a conspecific target with rather than without a head is consistent with the preference for the head over the headless image observed in Experiment 1a. In conclusion, the preference for the intact image relative to the headless one and the lack of a preference for the intact bird when paired with the head support the suggestion that the head or some property of it selectively controls schedule induced attack. Whether the low levels of attack on the headless images in this experiment reflect some minimal control by the torso or a tendency to attack a novel object or one similar to or associated with an effective target [Thompson and Sturm 1965] remains to be determined.

EXPERIMENT 3

The previous experiments indicate that the head of an intact conspecific image controls schedule induced aggression in White King pigeons. Although most aggressive pecks are directed toward the eye of the conspecific target, Looney and Cohen (1974) found suggestive evidence that the eye itself exerted little if any control over attack. In the next experiment, the target preference procedure was used to evaluate the role of the eye and each of four other head-related features (color, beak, head shape, and white head surface) in controlling schedule-induced aggression.

METHOD

Six pigeons from Experiment 2 (P8153, P8090, P8346, P8181, P8101, P81) were exposed to the target preference procedure with semi-randomly changing targets. Each bird was given a choice between the image of the standard intact (Fig. 1) and the blank screen for 3–5 sessions followed by a probe session involving a choice between the same intact bird and a degraded comparison image with a particular head feature deleted (Fig. 3). If the deleted aspect controlled attack, this would be reflected in a preference for the intact bird. If the feature were of little importance in the control of attack, the animals should show no preference. This sequence of baseline and probe sessions was used repeatedly to evaluate target features in the following order: color (black and white image with color around eye and on beak deleted), eye, beak, head shape (square shape with same area), white head surface (outline), and eye (re-exposure).



Eyeless



Beakless



Square
Head



Outline

Fig. 3. Black and white photographs of the rear view projected colored conspecific targets used in conjunction with the intact image (Fig. 1) in Experiment 3.

RESULTS AND DISCUSSION

Figure 4 plots for each bird the sensitivity index (based on total number of attacks) for each of the six probe sessions as well as the mean and range in sensitivity index for the baseline sessions that preceded those probes. As in Experiment 2, all pigeons except P8181 exhibited an extreme preference for the intact conspecific over the blank screen (Mdn mean SI = +0.97). Although the variability in baseline preferences for P8181 makes it difficult to evaluate the results of the probe sessions for that bird, the data for the remaining five birds indicated that no one aspect of the head selectively controlled aggression and that the relative contribution of each aspect varied somewhat across birds. In spite of individual differences between birds, certain properties of the head were generally more effective in controlling attack than others. The eye and the beak exerted the least control over attack, as evidenced by little preference for the intact target relative to ones without those features. Median SI across birds was +0.03 (range -0.16 to +0.26) and +0.08 (range -0.10 to +0.34) for the two eye probes respectively and +0.07 (range -0.11 to +0.18) for the beak probes. The white feathered surface of the head and head shape on the other hand exerted the most control over attack. Median SI across birds was +0.60 (range +0.32 to +0.80) for the outline probe and +0.50 (range +0.16 to +0.67) for the head shape probe. Color was intermediate in its effects on preference. The lack of control by the eye confirms suggestive evidence to that effect with silhouette targets [Looney and Cohen 1974]. Although the eye does not influence target preference appreciably, it is possible that that feature controls the locus of attacks on the head since aggressive pecks are directed at it. Additional experiments concerned with the locus of attack on degraded (eg. eyeless, beakless, etc.) conspecific images are needed to evaluate that point.

Without additional testing with other degraded images and combinations of images, it is unknown whether specific features of the head interact to control schedule induced aggression by a quantitative rule such as the Law of Heterogeneous summation [Seitz 1940]. In general, the data show that the effectiveness of a conspecific target in controlling schedule induced attack is inversely related to the physical distortion of the head. Removal of two relatively small but potentially salient features (eye and beak) had little effect on target preference whereas physically larger deletions and modifications of the head (outline and square head) resulted in greater but not complete preference for the intact target. The inadequacy of the outlined head may in part reflect a general tendency for pigeons not to react to two-dimensional line drawings of objects as they do to corresponding photographs, silhouettes, or the objects themselves. This is consistent with previous studies of schedule induced aggression in pigeons that have used line drawings for targets [Looney and Cohen 1974] and with Cabe's [1976]

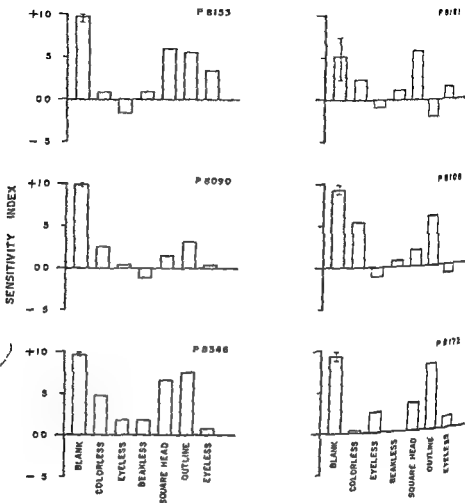


Fig. 4 Sensitivity index (SI) as a function of comparison image in order of presentation. Mean and range of SI's are presented for the baseline sessions (Blank) that preceded each probe. SI's for degraded comparison images are based on one day probes. SI's of +1, 0, and -1 correspond to a complete preference for the intact image, no preference, and a complete preference for the degraded comparison image.

ization in pigeons of positive transfer of discrimination learning from three-dimensional objects to photographs and silhouettes but not to line drawings. In summary the results suggest that the effectiveness of the head in directing attack is related to its physical integrity as a unit without regard to specific features. There may be a mass action effect (Lashley 1929) such that deletion or distortion of equivalent areas of the head (from a particular perspective) have comparable decremental effects. Such a perceptual mechanism would help to maintain the effectiveness of a freely moving conspecific target in directing attack in a complex environment.

CONCLUSIONS

The main finding of the present experiment is that the head of a visual image of a conspecific target selectively controls aggression induced by an intermittent food schedule in pigeons. This result is consistent with those of other experiments that have found that a gross change in a target affects schedule and shock induced aggression (eg Hyman 1976) and specifically that such changes in only the visual properties of a conspecific target influence schedule induced aggression in domesticated pigeons. The generality of the present findings with respect to feral pigeons (Yoburn and Cohen 1979) and other species of birds must be determined.

The selective visual control by the target's head is of interest in its relation to similar results obtained in field studies of reproductive aggression in other species of birds. In the reproductive context the head and head related features of an intruder bird are particularly effective in initiating aggression in passerines (Smith and Hosking 1955) and Larinae (Stout and Brass 1969). This apparent similarity between target control of different types of aggression in different species of birds suggests that aggression induced by an intermittent food schedule may be closely related to reproductive and other types of aggression. For pigeons and other birds there may be a common basis for visually perceiving an opponent bird in different contexts. Hostile pigeons for example may only attend to the aspect(s) of the opponent against which the aggressive contact is ultimately made. Within-species as well as across-species comparative studies of schedule induced reproductive and other types of aggression are needed to assess this possibility.

ACKNOWLEDGMENTS

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as stronger. They are exceptionally close to their parents while bullies show signs of alienation especially from fathers.

The work illustrates both the advantages and the disadvantages of this approach. Professor Olweus has demonstrated convincingly that each cluster of characteristics is shared by a sizable group of boys and that there is some stability over three years in spite of changes of school and teacher (although usually not peers). He concludes that there is an aggressive personality pattern resistant to change which probably relates to home factors. And perhaps there is a whipping boy personality too although this is less clear.

The kind of information which one gets from rating scales and questionnaires depends of course upon the questions asked. Professor Olweus has used a great deal of insight in both gathering and assessing information — insight gained no doubt from his previous studies. He looks at different kinds of aggression and finds bullies particularly inclined to teasing and verbal protest. He deduces that bullying provides a marked feeling of superiority and supremacy also a sort of satisfaction for vague revengeful impulses. He does not suggest why bullies should find this rewarding.

But the most insightful theoretical enquiry might fail to ask all the right questions and some puzzles remain which to my mind observation might elucidate. One of these relates to the apparent high self-esteem, popularity and lack of anxiety of the bullies. They seem in this sense well adjusted yet they are aggressive. Here teachers' comments are illuminating. They talk of a type that enjoys being the boss, cannot bear criticism, cannot bear losing and likes to create conflict. A few are described as having contact difficulties and making trouble in order to get attention.

Although Professor Olweus regards all this as "soft data" to be treated with caution, it nevertheless suggests a more coherent picture of a bully. We see a child trying desperately hard to prove that he has power over others; the desperation is evident in his excessive reaction to opposition. In my own study similar behaviour in nursery schools seemed an attempt to compensate for being (often repressively) at the bottom of the power hierarchy at home (Manning et al. 1978). In circumstances where they can present themselves as tough, powerful and successful where peers even admire and join them, such children appear confident and not anxious even though underneath they may feel themselves up against it. Professor Olweus has not yet analysed his findings on home backgrounds but the fact that bullies do not relate well to their parents is suggestive.

Nor are teachers' comments about contact difficulties necessarily at odds with the "hard fact" of popularity (judged by having two or three good friends). Observation suggests that such boys associate with one or two kindred spirits (who also enjoy the fun of teasing) but still have great difficulty in establishing normal friendly relationships with others.

Professor Olweus has done great service in revealing some of the facts

in destroying a number of myths and above all in stressing the seriousness and intractability of the problem. He argues convincingly that a bully situation is unlikely to sort itself out: bullies find it rewarding and whipping boys in allowing themselves to be intimidated provide the ultimate encouragement. He presses for intervention by the teachers both with the boys at school and with the parents at home and he makes useful suggestions on how this might be done. I believe these recommendations should be taken very seriously. It is hard for teachers to be faced with social work and child guidance as well as teaching but the problem is with us and is not likely to go away. The task will not be easy and the best means of approach is uncertain. I would still press for more observational evidence perhaps even guided observation by teachers and parents so that we can first come to grips with the real nature and motives of bullies and whipping boys alike.

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Manning M, Heron J, Marshall T (1978) Styles of hostility and social interactions in nursery at school and at home. An extended study of children. In Hersov I A, Berger M (eds) *Aggression and Anti Social Behaviour in Childhood and Adolescence*. Journal of Child Psychology and Psychiatry (Suppl 1). Oxford: Pergamon Press.

The Evolution and Chemistry of Aggression by D D Thiessen
Springfield Illinois Charles C Thomas 1976 pp xviii + 211

"It is impossible to even adequately cover the topics selected for presentation," states the author in his introduction. He is indeed right inasmuch as the book allows only superficial glimpses into his interesting topic. The analogy much stressed by the author that aggression is a form of competition has not received the critical in depth analysis one would expect. A similar superficiality also pervades Chapters 3 to 5 containing subject matter with which this reviewer is more familiar. In the chapter on Hormone Control of Aggression a discussion of the heterogeneous nature of the sexual process would be helpful for an understanding of the hormonal differentiation of sex and aggression. It would be appropriate to weave into the story first that the subcortical regions involved in gonadotropin release from the pituitary are different from those mediating

ing sexual (aggressive?) behavior patterns second that different brain regions are sensitive to different steroids and third that anterior hypothalamic lesions do not alter testosterone secretion but do prevent mating behavior The statement that testosterone in female mice tends to inhibit the aggression inducing effects of testosterone deserves to be expanded particularly in regard to the mechanism of prolactin release and its inhibition by dopamine The conclusion that high levels of progesterone may directly influence brain function and behavior or depress aldosterone formation does not contribute to an understanding of the actions of progesterone without better documentation Thus the selective uptake of progesterone into the limbic brain and the sedative effect of progesterone like agents are significant findings in a discussion on the aggression suppressing effects of this hormone Also progesterone does not control renin secretion nor does angiotensin II act on the glomerulosa of the kidney Progesterone stimulates renin activity indirectly because of its anti aldosterone effect which results in natriuresis

The fact that the area of drug effects is little understood although dramatic changes in aggression have been achieved by drugs should not license the author to write a rather uninspired chapter with so many errors and with the wrong emphasis To mention that mechanisms of action for benzodiazepines are almost completely unknown ignores the extensive literature on the cellular and regional central nervous action of this class of drugs In regard to aggressive behavior it would be more relevant to mention the attenuation of stress-induced noradrenalin turnover by benzodiazepines than to quote the reduction of serotonin turnover by oxazepam The emphasis on the provocative studies [which] strongly implicate cyclic AMP in modification of anxiety" is uncritical since the findings actually demonstrate that cAMP is not the common denominator of the effects observed In fact this hypothesis has been abandoned The selection by the author of noradrenalin and acetylcholine mechanisms involved in aggressive behavior is arbitrary Serotonin does not just play an historical role Mousekilling by rats can be inhibited by 5-HTP or pargyline and (irritable?) aggression is observed after inhibition of serotonin synthesis by p-chlorophenylalanine Also anti depressants with potent serotonin uptake inhibiting properties such as chlorimipramine inhibit stimulus bound attack by cats

Granted that the effects of dopamine and noradrenalin are often difficult to separate one or the other amine has been selectively accumulated by the administration of β -hydroxylase inhibitors and 6-hydroxydopamine Depletion of brain noradrenalin by 6-hydroxydopamine facilitates shock induced aggressive behavior

This book offers some interesting details which reveal the author's approach to the problem of aggression but it lacks a sharp focus on the problems it reports to discuss It also has far too many minor errors For instance Methedrone is methamphetamine (not amphetamine) and haloperidol is butyrophenone (not

phothiazine) Also haloperidol's major effect is to block dopamine receptors. Furthermore the subject index is inadequate. Hence this work is of small value to the serious student.

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Hormones and Aggression Vol 1 by Paul F Brain. Montreal
Eden 1977 pp viii + 126

This little book (69 pages of text and 33 pages of references) is one of a series of Annual Research Reviews edited by David F Horrobin at the Clinical Research Institute in Montreal. In an editorial introduction the reviews are described as "a new concept in medical and scientific publishing which will prove invaluable to those interested in finding the latest information on a topic. The introduction continues. Each topic is covered each year so that the successive annual volumes on any subject will provide a unique record of research in the field. The first volume in each series while concentrating on the past year's work attempts to provide a state of the art account and also gives a bibliography of key earlier references.

In view of the objectives and commitment of the entire series Dr Brain's book must be evaluated more critically than an isolated attempt to summarize a heterogeneous collection of experiments, naturalistic observations and clinical reports that in varying ways and to different degrees relate to the author's concept of "aggression." This concept is very broad indeed since it includes not only behavior involving overt fighting and threat but also hormonal influences on aggressive motivation. Despite much controversy concerning its final meaning Brain believes that the term aggression has some descriptive use and that it implies "(a) intent, (b) Potential injury to another organism and (c) Emotional arousal. The following table taken directly from the text represents a personalized preliminary classification of sub human aggressions based on the perceived utility of the behavior."

A Classification of Aggressions of Sub-Human Vertebrates in Terms of Perceived Utility to the Animal

1 Acquisition	<u>Object Acquired</u>	<u>Title</u>
	Prey	Predatory
	Food	
	Position in Hierarchy	Rank Related
	Territory	Territorial
	Mate	Mate Selected Relat
2 Aversion	<u>Object Removed</u>	
	Predator	Maternal
	Conspecific	Proximity Related
	Painful Stimulus	Pain Induced
	Fear	Escape Directed

None of the foregoing are considered appropriate for the classification of clinical studies and therefore these are subdivided into 1) those which assess aggression by questionnaire or interview and 2) those in which the behavioral characteristics of groups are classified on the basis of independent measures eg the use of the XYY chromosome abnormality the use of classes of violent nonviolent criminals clinical assessment of psychotic and non psychotic individuals participants in sport with a violent role and participants with more passive role etc

To the extent that he can understand them this reviewer sees little virtue in either of these taxonomic schemes which implicitly expose the absence of any unifying principles or trends that might justify the usage of aggression as a scientifically valid concept. The original fault lies in the literature itself where different authors have applied the same term to behavioral phenomena as different as killing of frogs by rats (raticide¹) and sexual exhibitionism by men. But the author is also culpable for he need not be captive to such vagaries and is under no obligation to include in his summary every study or category of studies that some author has idiosyncratically defined as dealing with aggression. Unfortunately this is more or less what Brain has attempted to do.

The book consists of an introduction with a statement of themes followed by a largely irrelevant single page chapter titled Hormones of Invertebrates and Aggression. The next five chapters treat the evidence on vertebrates in terms of different experimental approaches. For example Chapter 3 deals with effects of hormonal stimulation during early development on aggressiveness in adulthood. Chapters 4 and 5 review experiments on removal and replacement of hormones and associated changes in aggressiveness. Chapter 6 is concerned with natural variations in endocrine state (eg seasonal cycles sex differences strain differ

... etc.) and correlated variations in aggressive behavior or aggressive motivation. Chapter 7 reverses the approach and asks how engaging in aggressive behavior affects the secretion or release of hormones.

The internal arrangement of Chapters 3-7 is in terms of different glands or hormones, e.g. hypothalamic releasing factors (i.e. neurohormones) pineal adenohypophysis (TSH ACTH LH FSH PRL) thyroid adrenal medulla adrenal cortex and gonads. As a result the reader is confronted at points with an almost complete dearth of evidence (for example in relation to the pineal) and at others with an indigestible mass of facts such as those pertaining to the effects of castration on muricide behavior in killer rats, raticide in the same rat infanticide territorial fighting in gibbons, rank related fighting or even hyperaggressivity in dogs, male selection fighting in red deer, genital display (threat) in squirrel monkeys and rape in man.

In these five chapters the author evinces a curious tendency to strain at endocrinological grates while swallowing psychological camels. Each treatment of effects of testosterone is accompanied by separate discussions of aromatizable and non-aromatizable androgens. Whether testosterone must be aromatized before it can affect behavior is currently a matter of debate among experts but the distinction seems of little importance in the present book. Such recurring digressions appear particularly irrelevant in the absence of comparable concern for more important distinctions such as those between aggressive behavior and aggressive motivation. The eighth and concluding chapter deals with mechanism(s) whereby hormones influence aggressive behavior and here the reader is promised an attempt at synthesis with preceding sections of this review. What the synthesis amounts to is citation of evidence indicating that behavior depends on brain function and that brain function can be modulated by hormones. Many of the experiments cited have nothing to do with aggression and others are only inferentially related to behavior (e.g. binding of labeled steroid molecules by hypothalamic neurones). As a synthesis the chapter is singularly unsuccessful.

Concerted research on relations between behavior and the endocrine system is of relatively recent origin but is rapidly expanding into a new specialty that can be termed Behavioral Endocrinology. Pioneers in this field came originally from a variety of disciplines including psychology, zoology, neurophysiology and physiology as well as endocrinology. Only within the last two decades have we begun to attract specialists with technical skills and theoretical sophistication in both endocrinological and behavioral sciences.

Hundreds if not thousands of experiments have produced an impressive accumulation of empirical evidence and hundreds more are being published each year. Various aspects or portions of the field continue to be "summarized" or reviewed at regular intervals and when they are competently written these summaries serve a useful though temporary purpose.

The most serious need is not for still more summaries but for genuine theses that will attempt to bring some sort of order out of the accumulated and help us to distinguish those that are significant from those that are trivial.

We have less need for updated bibliographies than for organized attempts at theoretical interpretation that will provide intellectual structure and guide the understanding of existing evidence and the search for new facts.

"Hormones and Aggression" will not meet this need, but then it was not in an attempt to do so. A more fair and relevant criticism centers on the author's failure to face squarely his responsibility for clearly and explicitly defining the subject in such a manner that readers can assess the evidence independently, formulate alternative interpretations with possible theoretical and predictive sequences.

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A Guide to the Literature on Aggressive Behavior

Articles relating to the general problem area of aggression are scattered throughout the whole range of specialized journals in fields from A for anatomy to Z for Zoology. It is virtually impossible for a single individual to find all the articles which may bear on his particular interest. Information overload is of course a problem. However, an even greater problem is matching the interesting article with the interested reader. Aggressive Behavior will attempt to alleviate this problem by publishing a list of references in each issue. The reference list will be compiled from several sources. Each article listed in Psychological Abstracts and indexed under the following terms will be included:

- 1 Aggressive Behavior
- 2 Anger
- 3 Animal Aggressive Behavior
- 4 Attack Behavior
- 5 Hostility
- 6 Threat Postures
- 7 Violence
- 8 Frustration
- 9 Conflict

Each reference will be coded according to the index terms listed above and will be listed in alphabetical order by senior author. There are a large number of journals that publish articles related to aggression that are not covered by Psychological Abstracts. In order to find such references, the cooperation of all readers of this journal is needed. If each of the several hundred investigators concerned with the problem of aggression makes a habit of contributing to the literature search section of Aggressive Behavior, the search task of each of us will be made easier. If in your coverage of the literature you find an article about aggression in a journal that is not regularly abstracted by Psychological Abstracts, put the full reference on a 3 X 5 card and send it to the editor for inclusion in this section.

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Agonistic Rank, Aggression, Social Context, and Testosterone in Male Pigtail Monkeys

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Two groups of pigtail monkeys were merged; a third was formed, and individual males were introduced into a group in a series of experiments examining the effects of social context upon agonistic rank, aggressive expression, and testosterone levels. In the first experiment, two heterosexual groups, containing adult males unfamiliar to the other group, were merged. The two groups fought, and the smaller group was defeated. The alpha and beta males of the defeated group were singled out for repeated attack and both showed significant drops in circulating levels of testosterone. Both males were removed from the group during the first day, but testosterone levels did not recover to baseline levels for several days. The alpha male of the victorious group, on the other hand, showed a significant rise in testosterone, which was apparent only on the day following the merger.

In order to study the influence of previous social familiarity on male reception into a group, another group was formed by removing males from the victorious group and placing them in a separate enclosure. The males in the new group established a dominance hierarchy unrelated to their previous social ranks with one another. Three months later, each of the six adult males remaining in the parent group was individually introduced into the new group for one day or less.

Each of the males introduced into the new group accepted a social position at the lower end of the dominance hierarchy without regard to his previous rank relationships with the host males when they were all in the parent group.

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Even the alpha and beta males of the parent group were relegated to low rank positions in the new group despite having ranked over each of the host males since birth.

In contrast to the aggression directed at the unfamiliar males in the first experiment, a minimum of aggression was directed to the familiar males introduced into the new group in the second experiment. Although the males introduced accepted low social ranks, it appeared that each was readily integrated into the group with a minimum of aggressive interaction during the time he was scheduled to remain in the group. There were no significant changes in circulating levels of testosterone in any of the males during the introductions of familiar males to one another.

Key words: dominance determinants, group formation, testosterone, pigtail monkeys, familiarity and aggression.

INTRODUCTION

In studies of individual introductions of rhesus monkeys (*Macaca mulatta*) to established groups we have reported consistent defeat of the newly introduced animal, often accompanied by a depression of circulating levels of testosterone in male subjects [Bernstein et al 1974, Rose et al 1972]. Similarly, the merger of rhesus monkey groups has resulted in the defeat of one group by the other, with high ranking males in the defeated group showing plasma testosterone depressions, whereas the victorious alpha male showed a brief but dramatic rise in hormonal level [Bernstein et al 1974, Rose et al 1975]. In a few rare cases when introduced individuals were not defeated by the host group, successful defendants showed hormonal rises [Bernstein et al 1974], whereas mere membership in the victorious group did not produce hormonal rises in resident males not participating in vigorous successful attacks against intruders.

The present study was designed both to test for the generality of these findings to a second macaque (*Macaca nemestrina*) and to determine what influence previous social familiarity has upon the reception of an intruder into a group. If, in fact, dominance was an individual attribute expressed in social relationships, the knowledge of relative ranks in a previously long-established social relationship should allow for prediction of ranks after the introduction of animals into a new social setting. If, on the other hand, rank positions were a reflection of the current established social order, then past histories of rank relationships would not influence the new rank order established in a new social situation. If individual familiarity due to past association had no influence on the reception of a newcomer, then both social and hormonal responses to introductions should be the same for intruders regardless of past associations with animals in the host group. If, on the other hand, such associations did influence the reception received, there should be perceptible differences in receptions between familiar and unfamiliar animals introduced into a new social group.

METHOD

Unfamiliar Male Introduction

Two groups of pigtail monkeys were used in the first experiment. The first consisted of four adult males (Ob Z Ya C) four females and an infant whereas the second contained approximately 50 animals of all ages and both sexes including six adult male subjects (Z Kb Hb Lb Ec Tb). Both groups had been maintained undisturbed for at least six months prior to the period of study in outdoor compounds with access to indoor quarters.

The groups were merged by releasing the smaller group (group I) into the 10 m square compound containing the larger group (group IIa). The behavior of the ten males was observed and systematically scored using a standard vocabulary during the merger and for several hours thereafter. Additional observations were made during the following days.

Blood samples were drawn from each of the ten males six and four days prior to the merger and on the morning of the merger and on the first third and ninth days after the merger at approximately 1 000 hours in each instance. The collection of blood samples and the analysis of testosterone by radioimmunoassay were conducted using procedures that have been previously described (Gordon *et al* 1976). All assays were run in duplicate and the coefficient of variation of duplications was reported as 2.18% with sensitivity at 5 pg and blank values not significantly different from zero.

Familiar Male Introduction

The second experiment was conducted ten months after the first. Five adult males from group IIa (Hb Rb Ec Lb and Tb) two males from group I (Z and C) and several females were placed in another 15 m square compound to form a new group group III. These animals formed a new dominance hierarchy with Hb as alpha. Male Z failed to be integrated into the group and was removed. Dominance ranks were determined using the method of dyadic analysis of the directionality of agonistic encounters.

Three months after group formation the females were removed and six other males from group IIb (Kb Q Lc Yb Ya Zb) were removed one at a time placed in an individual cage for one week introduced to group III for one hour returned to their individual cage for another week and then returned to group IIb (Group IIb was the remainder of group IIa after III was formed). Removals from IIb were done at two week intervals so that only one animal was out of the group at any time. The order of introduction was not related to the rank of the animals which had changed since the removal of the animals to form group III so that Q who had been the alpha male of the group was now second to Kb.

The experiment was thus divided into four conditions with three blood draws in each condition. Baseline draws in the group took place minus 6, minus 4 days and at the time of removal. During the week in the individual prior to introduction, in the week following introduction, and in the week return to the group, blood samples were obtained at +24 hrs, +72 hrs, and 1 week. Behavior was scored during the first hour of introductions and summarized into 20 minute blocks. Data collection in this case used the introduced male as focal subject.

A summary of male subjects used in each of the two experiments and manipulation procedure appears in Table I.

RESULTS

Introduction of Unfamiliar Males

Shortly after the animals in group I were released into the compound the housed group IIa fighting broke out between the dominant males of the two groups. Q, the alpha male of the larger group, led his group and vigorously attacked Ob and Z, the alpha and beta males of the smaller group. Both Ob and Z received high levels of noncontact and contact aggression and displayed reciprocal aggression to the subordinate males of their own group. The attacks on Ob and Z were persistent and severe, and both animals received multiple wounds and had to be removed from the compound within two hours after being introduced.

The other two introduced males, Ya and C, received comparatively less noncontact aggression and very little contact aggression and engaged in nonagonistic social interactions with members of group IIa. In fact, within a few hours after the introduction, Ya repeatedly mounted a female and was no longer involved in agonistic episodes. C was the only introduced male to exhibit more noncontact aggression than he received, and this was directed primarily toward three group IIa males (Kb, the beta male of group IIa; Hb, and Rb). Although C generally avoided group IIa members, he would threaten any animal approaching the corner in which he spent most of the time. C was removed during the night for protection and on return to the group fought briefly with Q. He was removed again during the second night and was attacked by Kb on return, defeated, and removed to avoid further injury. Ya was the only male to remain with group I, and of the four males from group I, Ya was the only one who had lived in group IIa within the last five years.

The two males who were clearly defeated by the larger group, Ob and Z, each showed a dramatic fall in testosterone level. The mean measures and the three follow-up measures are shown in Table I. A *z* score was calculated for all follow-up measures to test for significance. Figures 1 and 2 express testosterone concentrations as the percent of the mean value for the period of the study and

TABLE I Adult Male Subjects in Each of the Study Groups

Unfamiliar Male Experiment		Procedure
Subjects		
Group I	Group IIa	Groups I and IIa merged
Ob	Q	
Z	Kb	
Ya	Lc	
C	Rb*	
	Lb*	
	Yb	
	Hb*	
	Zb	
	Ec*	
	Tb*	

Conclusion: males were drawn from group I and group IIa to establish group III. Asterisks designate males forming group III. Males Ob and Z of group I were not used in the second experiment.

Familiar Male Experiment		Procedure
Subjects		
Group IIb	Group III	
Kb	Hb	Each group IIb male was individually introduced to group III for 24 hours or less
Q	Lb	
Lc	Rb	
Ya	Tb	
Yb	Ec	
Zb	C (removed during first trial)	

Both Ob and Z show falls to less than 20% of mean values following introduction of males. Scores of 5.9 and 2.8 are significant ($P < 0.001$ and $P < 0.01$ respectively). The hormonal levels of the two undefeated males, C and Ya, fluctuated during the period of the study but all of their measures following introduction were within one standard deviation of their mean baseline values. (Defeat was defined as having occurred when the subject crouched, emitted submissive signals, and no longer responded with aggression to aggressive signals or attack or took any active steps to fend off attack.)

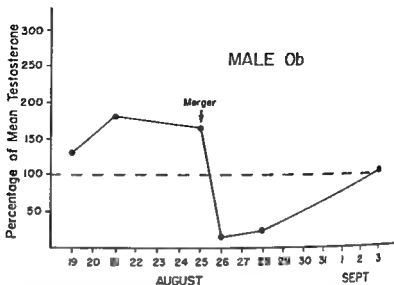


Fig 1 Testosterone levels of alpha male of the defeated group when two σ^7 were merged. All points are expressed in terms of the percent deviation from grand mean. Group merger occurred on 25 August immediately following the last baseline measure.

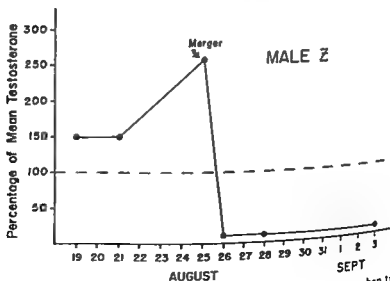


Fig 2 Testosterone levels of the beta male of the defeated group when two groups were merged. See caption Figure 1.

The alpha male of group IIa Q who led the attack on the group I males showed a brief rise in testosterone (see Table II and Fig.3) to a value almost two and one half times greater than his mean value for the period of the study (z score of 9.0 significant $P < 0.001$). Neither the beta male Kb nor any subject male in group IIa with the exception of Ec showed a significant hormonal rise on the day following the introduction. Male Em did show a significant 300% rise in testosterone although he was only observed to participate in a few agonistic episodes (z score 8.32 significant $P < 0.001$). Significant drops in Hb's levels and the rise in Kb's levels did not seem to relate to the group merger but rather to events within group IIa itself.

Introductions of Familiar Males

In the second experiment the social order of group III was maintained during each of the introductions of group IIb animals. Despite the fact that both Q and Kb had been dominant over all of the group III males since their births and up until this time they were removed from group IIb all of the group IIb males yielded immediately to Hb as the alpha male in group III. There were no massed attacks against any of the six familiar intruders although signs of tension [see Maxim 1978a,b] such as yawning and puckering [Bernstein 1970 elsewhere described as LEN Kaufmann and Rosenblum 1966 or jaw thrust Bobbit and Jensen 1964] were observed throughout the first hour. Virtually no aggression was observed during the introduction of Lc who (as also with Ya and Zb) was quietly accepted.

Table II Testosterone Values (ng/ml) of Males Prior to Group Merger and Changes

Subject	Mean baseline	+24 hours	+72 hours	+1 week
Group IIa				
Q	4.36	14.20*	6.89	3.35
Kb	17.17	16.34	24.99	32.00
Hb	17.99	10.1*	17.95	12.12
Lb	24.34	34.14	23.03	23.93
Tb	2.98	1.43	1.96	1.46
Ec	3.69	13.13	3.83	5.67
Group I				
Ob	26.08	1.58	4.18*	11.19
Z	19.25	1.23	1.24	1.37
C	16.08	26.92	13.16	19.78
Ya	8.62	3.17	3.02	6.47

Significant z scores at $P < 0.005$

Attack and Defensive Behaviors in the Albino Mouse

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Attack by dominant male colony mice on intruders included chasing and lateral attack behaviors, while the corresponding intruder behaviors were flight, boxing, and checking. Both of these are similar to the attack and defensive behaviors of colony rats and intruders. However, mice did not show a significant constraint on bites to ventral areas and the rat defensive behavior of lying on the back, which is effective because of this constraint, was rare. The corresponding on-top behavior of attackers was almost absent in mice. These findings strongly support the view that intraspecific attack and defensive behaviors and target sites for bites are interrelated factors facilitating effective but nonlethal agonistic interactions in murine rodents.

Key words: fighting, aggression, attack sites, defense, mouse

INTRODUCTION

Several independent analyses of attack and defensive behaviors in different animal species [Geist, 1971; Blanchard et al., 1977a; Blanchard et al., 1978] suggest that intraspecific fighting has a distinctive topography which is based on the adaptive value of specific attack and defensive acts or strategies. In *Rattus norvegicus* (the common laboratory rat) the following factors appear to operate in shaping the main features of attack and defense. The basic factor is a nonrandom distribution of bite targets on the body of an attacked conspecific, such that bites are seldom made on the ventral trunk. When bites are made in this area, they

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generally result in damage to vital organs and extrusion of intestines or at the very least a very high risk of peritonitis. Death tends to follow quickly even from a single bite. Thus a tendency for attackers to avoid such bites is obviously adaptive when there is a substantial probability that the attacker and defender rats are closely related—a situation which may be normative for colonial *Rattus norvegicus* groups. The constraint on bites to the ventrum is at least partly independent of the behavior of the bitten animal and may extend to total cessation of biting when only the ventrum is available to be bitten [Blanchard et al. 1977b].

The major defensive reactions of rats consist of boxing in which the defender rises or sits on hind limbs facing the attacker and lying on the back. Both of these reactions may be interpreted as adaptive because the primary area exposed to the attacker is the ventrum which involves little danger of direct bites while the more vulnerable back sites are concealed. In addition boxing is an especially effective tactic because protection is afforded by the use of the mystacial vibrissae which are fanned forward and interposed between the defending rat's head and the snout of the attacker.

The topography of attack is also related to the attacker's tendency not to bite the ventrum and to the specific defensive reactions used by the attacked animal. Dominant colony animals tend to make lateral attacks against boxing defenders crowding with the side of the body against the defending rat. From this position it is easy to make a quick forward lunge around the defender bringing the attacker's snout into contact with the prime bite target—the defender's back. When the defender is lying on the back the attacker stands on top of it usually at right angles to the line of the defender's body and darts around or over the ventrum to bite at side and back areas as these become exposed.

This pattern of target sites, defender behavior, and attacker behavior forms a nexus in which each activity is functionally related to other major acts in the system. Geist [1971] has suggested a similar set of relationships in mountain sheep in which target sites and fight topography combine to produce a system of intra-species agonistic behavior which permits victory and defeat without serious risk of death to either combatant. In bears there may be differences in the topography of agonistic behavior and target sites of bites and blows during dominance fights as opposed to disputes arising over food; the dominance fights involving bites and blows to the heavily furred neck and ruff area [Blanchard et al. 1978].

If the pattern obtained in rats is typical of intraspecific agonistic behavior in higher animals it should be comparatively easy to detect a close functional relationship of target sites and attack and defensive behaviors in other species. Moreover, in the case of species fairly closely related to the rat it seems likely that some similar or identical patterns might have emerged from their common evolutionary background. The present investigations therefore assess the topography of attack and defense and the sites of bites and lesions in mice and the functional relationships among these factors in this species in order to evaluate the across-species generality of the agonistic pattern described in the rat.

The colony situations in which these behaviors are examined were designed to provide a polarization of attacker and defender behaviors [Blanchard et al 1977a]. In these situations the dominant colony animals display a pattern of attack behaviors that shows almost no overlap with the defensive behaviors displayed by intruders. They therefore provide an opportunity to experimentally verify the categorizations of attack and defensive behaviors suggested by Scott [1947] or of attack and submission as suggested by Ginsburg et al [1942].

EXPERIMENT 1

Methods

Subjects The colony and intruder animals were albino Swiss Webster mice bred locally from stock obtained from Simonsen Laboratories. Six colonies were established by placing one male and two female mice in each colony compartment. These animals had been weaned at 21 days of age and housed with like sex littermates until placed in the colonies at an average age of 150 days. When formal colony testing was initiated, the male mice of these colonies averaged 176 days of age and 41 gm in weight. The six intruder mice used in the filmed sessions averaged 91 days of age with a mean weight of 40 gm. The intruders had been weaned at 21 days of age and housed with male littermates until 20 days before the study at which time they had been separately housed in individual metal mouse cages (7.4 X 20 X 20 cm).

Apparatus The colonies were housed in translucent amber-colored plastic cages measuring 38 X 32.5 X 16.5 cm, covered with a wire mesh top. A layer of wood shavings was used as bedding and was changed each week. Food and water were continuously available.

A Braun Nizo camera and Kodak Ektachrome Super 8 film were used to record the agonistic sequences in the first experiment. Supplemental lighting for these films was provided by a 100 W bulb in a reflector.

Procedure When the colonies were formed, each colony male was marked with Fuschian dye to facilitate identification during intruder tests. Three days after the colony was formed, the first of a series of preexperimental intruders was introduced into each colony for a five minute period. Within two weeks of receiving intruders on every third day, a steady base line for attack latency, bites and attacks on the intruders, as well as other attack behaviors, was obtained in each colony. The formal colony intruder sessions, which were filmed, took place on day 18 after the initial intruders were introduced.

For all intruder sessions, the females and any pups in each colony were removed prior to the introduction of the strange mice. During the formal colony sessions, an intruder was introduced into the colony cage, now occupied by only one colony male. Filming at 24 frames per second was initiated with the first attack seen and continued for the next 180 seconds.

The films were examined in slow motion and also on a frame by frame basis on a Goko film editor. The behaviors of both attacker and defender were classified by an experienced rater and their durations (or other appropriate measurements) were obtained. The behavior categories recorded were the following:

Attack Behaviors

- 1 Straight approach: moving in a straight line toward the other animal
- 2 Circle approach: moving in the direction of the other animal via an arc-like path and approaching to within 5 cm
- 3 Chase/pursuit of a fleeing opponent. If either a straight or a circle approach resulted in flight of the approached animal and the approach continued, it was scored.
- 4 Biting: frequency, duration, and the site on the opponent which was bitten were all recorded.
- 5 Bite chase: the bitten animal flees and the biter maintains his bite grip and moves with the fleeing animal.
- 6 Lateral attack: an animal moves laterally toward or in a tight circle around and within 2 cm of its opponent.
- 7 On top of: an animal stands over or on top of its opponent.

Defensive Behaviors

- 8 Flight: moving away from an approaching opponent.
- 9 Freeze: periods of immobility lasting more than 1/3 second.
- 10 Checking: turning to maintain one's orientation toward the attacking animal at a distance of less than 5 cm but greater than 1 cm.
- 11 Box: erect on the hind limbs with orientation toward the opponent.
- 12 On the back: lying on the back.
- 13 Turn to face: a turn to face the other animal which is in close contact.

In addition to these categories, characterized as attack behavior or as defensive behavior on the basis of a functional analysis of fighting in rats (Blanchard et al. 1977b), a final category of "Other" included such activities as brief periods of immobility (less than 1/3 second), exploration, self-grooming, drinking, etc.

After filming, intruders were removed from the colony enclosures and sacrificed with an overdose of pentobarbital sodium (Pembuto[®]). They were then covered with a commercial depilatory (NEET[®] hair remover) and refrigerated for 74 hours. Depilatory and body hair were then removed and lesions counted and catalogued by the site of damage. Pilot studies indicated that new lesions could readily be distinguished from lesions more than a week old, so the fresh lesions counted on intruders could reasonably be attributed to injuries received during the colony session. Lesions on the colony males, however, could have been made at any time. Therefore, observations of intruder bites on the colony males were used as the score index of target preference in these mice.

Statistical analysis of results involved *t* tests for measures meeting the usual requirements for parametric analysis. Other behaviors—usually those which were infrequent and not normally distributed in one or both groups—were analyzed by means of Mann-Whitney *U* tests.

Results

Attacker versus defender behaviors (film analysis) Film analysis of the intruder-colony mouse interactions indicated a consistent difference between the behaviors of these two groups of animals, as well as the sites on which they bit their opponents. Table 1 presents the proportion of time that colony mice or intruders spent in each of the measured behaviors. As this table indicates, colony males spent notably more time in straight approach, circle approach, chase, bite-chase, and lateral attack behaviors than did the intruders (Mann-Whitney *U* test: $U = 0$, $N = 6$ and 6 , $P < 0.001$ in each case). Although on top behaviors were somewhat more common for the colony mice, this behavior was seldom seen in either group of mice.

TABLE 1. Percentage of Time Spent in Given Behaviors for Colony Male Mice and for Conspecific Intruders in the Colonies

Behaviors	Mean percentage times ^a	
	Colony males (N = 6)	Intruders (N = 6)
Attack behaviors		
Straight approach	61*	01
Circle approach	14.4***	01
Chase	12.8**	00
Bite-chase	5.4*	00
Lateral	10.3**	01
On top	1.4	07
Active defense		
Boxing	4.8	13.0
Checking	00	5.2*
Turn to face	01	1.4
On the back	01	07
Flight	3.4	25.4
Freezing	17.5	17.3
Roll-tumble	02	06
Other	19.8	29.8

^aIn each case the asterisks designate the group showing the higher level of that behavior.

* Colony male-intruder differences reliable at 0.05 level.

** Reliable at 0.01 level.

*** Reliable at 0.001 level.

and the difference was not significant ($U = 6$ $N = 6$ and 6 $P > 0.05$) The intruders spent reliably more time boxing ($t = 2.56$ $N = 10$ $P < 0.05$) checking ($U = 0$ $N = 6$ and 6 $P < 0.001$) turning to face ($U = 1$ $N = 6$ and 6 $P < 0.01$) and in flight ($t = 6.15$ $N = 10$ $P < 0.001$) than did the resident mice

This division of behaviors for mouse colony animals versus intruders obviously corresponds well to the division of behaviors as attack or defensive on the basis of colony male and intruder behaviors in rat colonies. It also agrees with the categorizations of Scott [1947] and of Ginsburg et al [1942]. All five of the behaviors for which colony mice were higher than intruders were similar or identical to those designated as attack behaviors in the rat studies while all of the four intruder mouse behaviors were typical also of rat intruders. Of the behaviors which did not differentiate the present resident and intruder mice two (freezing and on the back) had been designated as defensive on the basis of the rat results while a third on top was an attack behavior. All of these behaviors occurred at a much lower level in mice than in rats a finding in agreement with the finding of Grant et al [1963] of relatively little lying on the back (which they term full submissive posture) or standing on top (full aggressive posture) in the mouse. The remaining categories (roll tumble and other) did not differentiate the behaviors of resident animals and intruders in either rat or mouse colonies. Thus the present results suggest a very similar array of attack and defense behaviors for mice and rats with the exception that freezing and on the back behaviors typical of intruder rats appear not to be so typical of mice and the corresponding on top behavior of attacking mice is similarly reduced.

Additional evidence of similarity of attack and defensive patterns in mice and rats is provided by the sites at which bites occurred for colony and intruder mice presented in Table II. As this table indicates much more biting was typical of the colony male mouse than of the intruder ($t = 3.51$ $df = 10$ $P < 0.01$). In addition the sites bitten on the opponent animal also tend to vary systematically with the

TABLE II Percentage of Bites as Given Target Sites

Target site	Bites by colony males	Bites by intruders
Anterior back	13.2	8.0
Posterior back	64.7	7.8
Hind limbs	7.3	10.9
Front limbs	1.5	0.0
Tail	0.3	37.4
Head	1.8	6.5
Abdomen	8.6	1.1
Thorax	2.6	13.3
Mean number of bites	64.0	

status of the biting animal. Colony male mice made the majority of their bites in the posterior back area of the intruder while the intruders bit the head of the colony animal. Both posterior back bites ($t = 8.74$, $df = 10$, $P < 0.001$) and head bites ($U = 0$, $N = 6$ and 6 , $P < 0.001$) were reliably different for the two groups of mice. Colony males also made fewer bites to the ventral body surface (abdomen and thorax) than they did to the dorsal body surface (anterior and posterior back) ($t = 4.54$, $df = 5$, $P < 0.01$).

Both of these findings — a tendency for colony animals to bite dorsal areas of the intruder and for the intruders to make their many fewer bites on the head and ventral areas of the colony animals — agree with the patterns of bites seen in interactions of colony and intruder rats. Moreover, the finding that ventral areas are less often bitten than dorsal areas is also similar to the findings of rat encounters. Some differences do appear, however. First, the primary target for bites by colony rats on intruders is the anterior back rather than the posterior back site favored by mice. Although few ventral bites were seen in the present situation, there were somewhat more of these than are typically seen in rat encounters. As a general summary, however, it is apparent that the present mouse data generally repeat features of a systematic distribution of bites in attack and defense by rat colony animals and intruders.

Interaction of attack and defensive behaviors of the mouse. Table III presents the proportion of bites preceded by a given behavior of the bitten animal or of the animal making the bite for bites by both colony males and intruders. As this table indicates, most of the bites made by colony males on intruders occurred while the bitten animal was fleeing. Flight was clearly an extremely dangerous behavior for the intruder, as nearly 60% of bites were made during intruder flight. Although such flight accounted for only about 25% of interaction times. Thus, though flight might be expected to result in the removal of the intruder in more natural situations, it is obviously a poor defensive behavior in the inescapable colony situation.

Boxing was also a dominant intruder behavior, occurring during 23.0% of the observed periods, but it was associated with a much lower rate (14.1%) of bites received. The other major intruder behavior, freezing, was associated with an even lower level of bites. It might be noted, however, that such a comparison does not unequivocally indicate the value of defensive behaviors in thwarting bites, since freezing and some other activities (Other) observed primarily occurred while the attacker was at a distance or temporarily failing to press its attack.

The three major behaviors of the attacking animal, which were most clearly associated with bites made by these mice on the intruders, were chase, the lateral attack, and approaching (straight plus circle). Of these behaviors, the lateral attack and chasing were especially likely to result in a bite, since they occupied only 7.31% of the times analyzed but resulted in nearly 60% of bites made by the animals.

TABLE III Percentage of Bites Preceded by a Given Behavior

Behavior	Colony male bites		Intruder bites	
	Colony male preceding behavior	Intruder preceding behavior	Intruder preceding behavior ^a	Colony male preceding behavior
Approach (straight + circle)	12.50	0.00	0.00	1.75
Lateral	17.71	0.26	0.00	10.00
On top	5.21	1.56	3.75	2.50
Chase	40.62	0.00	0.00	5.00
Bite	4.42	1.30	0.00	73.75
Box	4.43	14.06	11.25	0.00
Checking	0.00	0.00	5.00	1.87
Flight	0.00	59.37	63.75	7.40
On the back	2.04	3.39	1.75	2.50
Roll/tumble	1.04	1.30	3.75	0.00
Freeze	0.00	3.91	0.00	0.00
Other	10.94	10.15	10.00	2.40

^a Since an intruder facing away from his opponent must necessarily engage in a turn-to-face movement in order to bite, that category was omitted from this analysis. Where applicable, the category of behavior preceding the turn-to-face movement was counted as preceding the intruder bite.

The behavioral antecedents of bites made by the intruding mice on the colony animals were even clearer. Nearly two thirds of intruder bites occurred just after the intruder had been fleeing, and nearly 75% of all bites occurred just after the colony male had bitten the intruder. Thus, while bites on intruders occurred after sequences of attack behaviors by the colony animals and defensive actions of the intruders, bites by intruders occurred just after the intruders had been bitten by the attacking colony males.

Attack and defense patterns in mice and rats. This pattern of findings provides overwhelming evidence of a basic similarity of mouse and rat intraspecific attack behaviors. The exceptions to this pattern are also systematic. Mice, in comparison with rats, appear to have a less definite preference for dorsal target sites for bites. Also, intruder mice show much reduced levels of lying on the back and of freezing on top behavior. Since the strategic value of lying on the back depends on a constraint on bites to the ventrum, these findings may all reflect the comparative lack of such a constraint in mice. Experiment 2 therefore examined bite targets on anesthetized mice.

EXPERIMENT 2

Experiment 2 was designed to obtain information on the possibility of a limitation on bites to the ventrum of conspecifics in mice which is independent of the behavior of the attacked animals

Method

Subjects The colony animals were those used in Experiment 1 and the intruders were 24 male mice of this same strain averaging 148 days of age with a mean weight of 40 gm. These intruders had been reared under conditions similar to those of the intruders in the first experiment

Apparatus The colony cages were those used in Experiment 1. Also a platform was used to secure some of the anesthetized animals. This was an X shaped section of 6-cm plywood with its rectangular outline measuring 20 X 15 cm. A 2.5 cm hole was fastened to each of the four exterior corners of the platform to which the limbs of the anesthetized animal could be fastened by means of rubber bands

Procedure The sites of bites and wounds were determined for four groups of specific intruders into the mouse colonies. The first group was unanesthetized and unrestrained — equivalent to the mice used in the film analysis. The remaining three groups were all heavily anesthetized (90 mg/kg sodium pentobarbital): the first in one of these groups were not tied down but simply placed on their sides in the colonies. The remaining anesthetized mice were tied to the X shaped platform either with the dorsal surface exposed or with the ventral surface exposed. Intruders were placed individually into one of the six colonies; the order of introduction of the mice of the four groups being varied according to a predetermined random order. All stimulus mice were used for a single session. The sessions were six minutes in length beginning with the first bite of the colony male on the intruder.

After being removed from the colonies all intruders were sacrificed and NLET used to remove their hair. Lesions were then counted and categorized by site.

Data

Target sites on dorsally and ventrally presented intruder mice. Table IV presents mean number of lesions on each type of stimulus animal plus the percentages of lesions at each target site for the different stimulus groups. As this table indicates colony mice made reliably more bites at unanesthetized intruders than at anesthetized but unfixed animals ($t = 4.03$ $df = 5$ $P < 0.01$) or at the ventrally presented group ($t = 3.55$ $df = 5$ $P < 0.05$). Although considerably fewer bites were made at the fixed dorsal group than at the unanesthetized group this difference was not statistically significant ($t = 1.60$ $df = 5$ $P > 0.05$). Within the anesthetized stimulus groups there were no reliable bite differences although

TABLE IV Proportion of Lesions at Given Loci for Three Anesthetized and One Unanesthetized Stimulus Mouse Groups

	Locus						
	Head	Anterior back	Posterior back	Limbs	Thorax	Abdomen	Tail
Unanesthetized	4.5	14.9	54.1	13.2	3.1	9.7	0.9
Anesthetized							
Unfixed	37.9	12.5	17.9	12.8	8.7	9.5	0.4
Fixed dorsal	68.1	16.6	5.9	11.6	0.0	1.1	0.6
Fixed ventral	70.6	0.0	0.0	3.3	20.9	5.2	0.0

more than twice as many bites were made at the dorsal stimuli than at the ventrally presented animals.

Comparison of the distributions of bites on the bodies of the three anesthetized groups in comparison to the unanesthetized group indicates a shift from the sites most often bitten on unanesthetized intruders to a consistent tendency to bite at the heads of anesthetized animals. This pattern is perhaps even more pronounced in rats where about 75% of bites on anesthetized conspecifics are on the head (Blanchard et al. 1977b). The differences in head bites to unanesthetized as opposed to anesthetized mouse targets were reliable ($U = 0$, $N = 6$ at $P < 0.05$ for each comparison). It seems very likely that this difference is attributable to protection of the head by active use of the vibrissae in unanesthetized mice or to active avoidance of the snout and teeth of the opponent animal by mice attacking unanesthetized mice.

However, in contrast to the pattern obtained in rats, bites at the ventrally presented stimulus mice were frequently made on ventral trunk areas. Such bites accounted for 36% of all bites seen in this group, a figure equivalent to the 36% of bites made to back areas in the dorsally presented stimulus group. It should be noted that fewer (though not reliably fewer) total bites were made at the ventrally presented mice, but these data certainly do not suggest any limitation of ventral bites in mice that is equivalent to that seen in rats.

Another comparison relevant to this point may be found in the numbers of bites to ventral as opposed to dorsal trunk sites on the mice that were unanesthetized but not fixed. Since the attackers could turn these animals freely to select targets, the finding of 22.8% dorsal trunk bites versus 13.7% ventral bites may suggest some preference for the dorsal targets. It does not, however, imply a effective constraint on bites to the ventral areas.

These data then suggest that of the two factors postulated to influence the form of defensive behavior in rats one is also effective in mice while the other is less important. Defending rats fan their vibrissae forward and interpose these between the attacker's snout and their own vulnerable head (and sometimes body) as it is. If the vibrissae are removed or even anesthetized this protection is reduced and more bites especially to head areas result [Blanchard et al. 1977c]. The present finding that anesthetization produces a striking increase in bites of a mouse to the head of a conspecific clearly suggests that the vibrissae and their use serve a similar protective purpose in mice. An additional and perhaps even more important mechanism that protects the head of unanesthetized mice is the danger of retaliatory biting. An attacker bite toward the head of a defender involves a substantial risk that the defender will retaliate by biting the attacker's snout.

Since the head of the attacked mouse is protected by both of these mechanisms it is extremely adaptive for a defensive mouse to use the boxing defense to a specific opponent. During boxing the defender presents its head, vibrissae and teeth to the teeth of the attacker while concealing its own back. An upright stance also permits the quick pivot necessary to follow an attacker's lunge around toward the defender's back. Thus the adaptive value of boxing and of the circling and lateral attack which is the usual attacker response to a boxing defender appears to be related in both mice and rats to the relative invulnerability of the defender's head.

While a mouse is lying on the back however maneuverability of the head is very limited. Thus use of the vibrissae and the danger of retaliatory biting is limited when an animal is in this position. This tactic is therefore quite dangerous in terms of risk of bites unless it is extremely unlikely that even an unprotected ventral area will be bitten. In rats almost no biting of unprotected ventral sites occurs; this constraint therefore makes the tactic of lying on the back effective. In mice a decrease in lying on the back is understandable in the context of sharply reduced effectiveness of limitations on bites to the ventrum.

The present results therefore suggest that of the two major phenomena which shape attack and defensive behaviors in the rat one is also important in the mouse. The other a constraint on bites to the ventrum is not of major importance. It is not clear why mice should be so different from rats in terms of readiness to bite the ventral area of a conspecific. Perhaps this is related to the degree to which these species typically live in closely related groups. Another possibly related factor is that mouse wounds tend to be punctate and therefore less serious than the tearing wounds made by rats thus making a constraint on ventral bites less necessary in mice.

The significance of these findings however is not just that mice resemble or fail to resemble rats in their agonistic behaviors. What is significant is that these

data provide additional and unequivocal support for a view that the topography of each specific agonistic behavior for a given species is a predictable component of a pattern linking behavior, body structure, and the social and physical environment of that species. If one component of this pattern changes, such as the constraint on bites to the ventrum of a conspecific, then this alters the adaptive function of other components in the system; in this case the defensive behavior of lying on the back and the on top attack. None of these three differences in the agonistic behaviors of mice as compared to rats is understandable in isolation. In combination they provide insight into the adaptive function involved in the evolution of a complex behavior system.

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The Reinforcing Value of Several Types of Aggressive Behavior: A Review

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Field observations of "surplus killing" and laboratory studies of operant performance rewarded by prey killing opportunities suggest that predatory behavior is positively reinforcing. Similarly, both repeated encounter and operant performance studies suggest that intraspecific aggression can be positively reinforcing for successful aggressors. While a few studies suggest that defensive aggression under aversive conditions may also be positively reinforcing, it appears that when appropriate response modes are available, escape and/or avoidance are preferred to attack. Studies of the reinforcing properties of aggression-eliciting brain stimulation are in general agreement with these conclusions, but methodological problems with these latter observations render them less compelling.

The progressive escalation of aggression seen in "warm up effects" of birds and fish, "priming effects" of mice, and ecstatic violence of humans may be analogous processes based on the positively self-reinforcing characteristics of some kinds of aggression. The transient reductions of aggression which appear as refractory periods and satiation effects in a variety of species may reflect temporary reductions in the reinforcing value of aggression. All these temporal effects must be considered in the evaluation of experiments on the reinforcing value of aggression. More generally, it is probable that these temporal fluctuations reflect the operation of common motivational processes (aggressive states) which regulate overt aggression by changing its reinforcing value.

Words: aggression, predation, reinforcement, situation, time course

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INTRODUCTION

The rediscovery of predatory [Myer 1964] and shock elicited defensive aggression [Ulrich and Azrin 1962] in laboratory rats facilitated by the simultaneous popularization of ethological views [eg Lorenz 1966] has promptly renewed and continuing interest in aggression among laboratory investigators of animal behavior. A general if not complete consensus has arisen that several quite distinct forms of aggression may be distinguished on the basis of specific typical response topography and a variety of other indicators [eg Moyer 1974]. However, the precise number and exact characterization of these forms is still a matter of dispute. The examples chosen for this paper can be categorized relatively unambiguously as either predatory intraspecific or defensive (irritated) aggression [cf Moyer 1976].

That aggression may be used by animals as an operant to attain other ends, eg acquisition of resources or removal of a threat, is not surprising. However, a number of the recent laboratory studies have also provided experimental evidence which supports the ethological contention that, under appropriate circumstances, performance of some of these forms of aggression is positively reinforcing in itself. That successful aggression can be an intrinsically rewarding experience for the aggressor is a striking and, to some, counterintuitive proposal. Some studies demonstrating the positively reinforcing aspects of aggression *per se* have already been reviewed [eg Johnson 1972, Baenninger 1974, Rasa 1976, Hinde and Roper 1978]. Nonetheless, reexamination of the experimental observations to date is warranted by: 1) Some recent significant contributions to the literature; 2) the potential importance of this not yet widely appreciated phenomenon, particularly with regard to the temporal patterning of aggressive behavior and the possibility of relating this work to some observations on human aggression.

Temporal Patterns of Aggressive Behavior

The experimental analysis of the reinforcing properties of aggression is complicated by the variety of temporal patterns occurring in aggressive behavior. These patterns have both methodological and theoretical implications and must therefore be reviewed here briefly. There are at least 3 of these temporal effects that are of concern.

Warm up and priming effects. In the presence of a continuously available target birds [eg Hinde 1954, Curio 1975] and fish [eg Pecke et al 1971] show initial transient increases in the rate of mobbing or rate of intraspecific attack, respectively. These warm up periods often last from 1-3 minutes but may continue for 30 minutes or more, particularly in fish [eg Pecke et al 1971]. I am unaware of similar data for mammals. However, a possibly related observation in mice is the priming effect [Hogan and Roper 1978]. A brief aggressive encounter transiently facilitates operant performance for the opportunity to perform additional aggressive behavior [eg Lagerspetz 1964, Tellgren and Hinde 1971].

9) These effects may be comparable to anecdotal accounts of human beings where aggressive behavior escalates itself into a violent frenzy [eg Baenninger 1964; Zimbardo 1969]

Bout effects In the presence of a continuously available target aggression like many other behaviors tends to occur in bouts. A closely spaced group of individual attacks is often followed by periods of little or no aggressive activity. In rats these refractory periods vary from a 2-3 minute pause following a single bout attack [Adams 1976] to a 10 minute pause after a 5-6 minute bout of attack [Blanchard and Blanchard 1977]. For hamsters the mean bout duration is approximately 2 minutes while the mean interbout interval is approximately 15 minutes [Potegal et al 1976]. Hogan et al [1970] report that fighting behavior displays occurring at a mean of 15/hour tend to cluster in groups of 8 implying that the mean interbout interval is approximately 20 minutes.

Satiation effects Some studies have indicated that if an animal is allowed to attack a target ad libitum for an extended length of time the rate of attack decreases relatively rapidly. Thus in mice aggression decays times [time for attack to reach 37% (1/e) of its initial value] of approximately 30 minutes can be calculated from data of Levine et al [1965] and of Thurmond [1975]. If after an interval animals are again allowed access to a target the amount of aggression in times with increasing intervals. Estimates of the minimum interval necessary for recovery from aggression satiation in mice which must obviously be dependent on the degree of satiation range from 2 days [Scott and Frederickson 1951] to weeks [Krsiak and Janku 1969]. Connor summarizes the most systematic study of this question in remarking that in his experiments 1) the satiation effect was of the aggression scores of mice to an asymptotic floor in four hours less and 2) the deprivation effect elevated scores to an asymptotic ceiling in hours or less (Connor 1971 p 225). Among various species of fish aggression recovery times of 11-28 minutes can be calculated from data of Peeke [1969] and of Peeke and Veno [1973] and times of 2-5 minutes from data of Hieligenberg (for review see Hieligenberg 1974). Recovery times vary from less than 1 day [Fizler 1971] to more than 5 days [Van den Assem and Van der Molen 1969; Peeke and Ke 1972; Peeke et al 1971]. It thus appears that in a number of different species aggressive behavior is relatively quick to satiate and slow to recover. Similar bout periods and satiation effects have been clearly established in animal behavior [eg McGill 1969; Karen and Barfield 1975]. The relationship of these temporal effects in aggression to each other or to those in sexual behavior remains unclear. The methodological significance of these three parallel effects in aggression follows from this possibility. The mechanisms which determine the timing of aggression in experimentally uncontrolled aggressive encounters may influence or override experimentally imposed [eg operant] constraints. Their theoretical significance lies in the possibility that they may be underlying and eventually not as impediments to the experimental analysis of aggressive

motivation but as manifestations of fluctuations in aggressive motivation. This possibility is discussed in greater detail in the last section of this paper.

Reinforcing Value of Predatory Aggression

Field studies of feral predators have revealed the existence of "surplus killing" by foxes and other mammalian carnivores [Errington 1967 Kruuk 1971]. In these instances the predators kill far more prey than they can eat at one time after which they leave the scene without attempting to cache the excess dead prey. In other instances predators (eg. lynx) will kill but rarely if ever eat predators belonging to sympatric species (eg. foxes). Kruuk offers a number of interpretations of the adaptive significance of surplus killing. The adaptive advantage of a predator of reducing the number of competitors seems obvious; the advantage of destroying large numbers of prey is less obvious. It is possible that surplus killing reflects the practice of an enjoyable predatory skill which becomes maladaptive under the ecologically unusual circumstance of abundant, easily accessible prey. Even if surplus killing could be shown to have some adaptive value it would still not obviate the necessity of determining the proximal behavioral means (eg. the motivational mechanisms) by which the distal evolutionary ends are served.

In the laboratory cats [Roberts and Keiss 1964] and rats [Myer and White 1965] will learn T mazes for the opportunity to make predatory attacks on rats and mice respectively. Rats will also bar press [van Hemel and Myer 1970 van Hemel 1972] for the opportunity to kill mice. It is important to note that the subjects in these experiments had never eaten prey objects prior to the study and were not allowed to do so during the experiments. Indeed, several lines of evidence indicate that in many species predatory hunting and killing belong to a motivational system separate from that of feeding. In the course of development the two systems ordinarily become associated through learning (for a brief review see Adamec 1976). Field observations suggest and laboratory studies confirm that predatory killing can be positively reinforcing whether or not the prey is eaten.

Reinforcing Value of Intraspecific Aggression

There are anecdotal accounts of domesticated cats [Ewer 1968 p. 156 Levine 1971], meerkats [Ewer 1968 p. 340] and buntines [Andrew 1957] which appeared to go looking for a fight with conspecifics. In the laboratory the reward value of intraspecific aggression is suggested by the numerous demonstrations that winning or losing paired encounters can increase or decrease subsequent attack rates in fish [Heiligenberg 1964 McDonald et al. 1968] mice [Uhrich 1940 Ginsburg and Allee 1942 Kahn 1951 Scott and Marston 1964 Lagerspetz 1964 Brain and Poole 1974] or rats [Seward 1946]. The reward effect in attack initiation occurring after defeat is probably a straightforward aversive effect due to punishment [cf. Hudgens and MacNeil 1970]. Increases in attack rates following victory are more problematic. In these experiments the

nothing contingent on winning. Therefore the increases in attack rate in victorious animals suggest that successful attack may be intrinsically rewarding.

An alternative to the positive reinforcement explanation of these paired encounter results has been proposed by Leshner and Nock [1976]. They found that only mice whose aggressive encounters were interrupted before they had achieved victory (submission of their opponents) showed increased aggression. Since mice which were allowed to fight to victory showed no change in aggressiveness they interpreted the increases in aggression in terms of unfulfilled expectancy of victory on the part of the interrupted mice. There is an interesting hypothesis although it is unclear that an expectancy which remains unconfirmed should be necessarily result in a more rather than a less vigorous pursuit of that expectancy. Alternative explanations of these data exist. For example it is possible that the non interrupted group which had considerably longer fight durations (up to an hour) may have satiated on fighting. In any event Leshner and Nock have raised the important consideration that the reward value of aggression may involve not only the performance of and perhaps immediate sensory feedback from the motor acts of aggression but also the capitulation of the opponent.

It can also be argued that subjects in the paired encounters learned to avoid pain inflicted by their opponents by attacking them first. To demonstrate more clearly the appetitive nature of aggression it is necessary to show that organisms will learn and perform operant behaviors to provide themselves with intraspecific attack opportunities when they could easily avoid such interactions by not performing the operant. Fighting fish (*Betta splendens*) and other fish species will learn to produce operant responses for the opportunity to display aggressively to live or model conspecifics or to mirrors [Thompson and Sturm 1965, Hogan 1967, Hogan et al 1970, Runc 1977]. These results appear to be somewhat ambiguous however. Some authors report that the operant performance is highly correlated with aggressive display [Thompson 1963, Melvin and Anson 1969, Davis et al 1974, Rhoad et al 1975, Bols 1977] while others find that operant responding may continue after the display has habituated [Baenninger 1970, Baenninger and Matileman 1973, Johnson and Johnson 1973, Turnbough and Lloyd 1973]. In these latter studies, some other aspects of the visual presentation presumably also provided some reinforcing stimulation. A second confounding factor in those studies of fighting fish which used a response independent mirror image presentation is that such a fixed mirror image is less reinforcing than a response contingent mirror image [Baenninger and Matileman 1973]. Mirror images are more aversive than live antagonists [Bols 1977] since the mirror images do not support the coordinated display interaction that occurs between two live antagonists [Simpson 1968].

Stronger evidence of aggression-contingent operant performance can be found in studies involving actual attack rather than display. When appropriate experimental precautions are taken to insure the relatively painless victory of the aggressor the demonstration of attack preference becomes possible. For the

opportunity to perform aggressive behavior against conspecifics birds will peck keys [Thompson 1964 Cole and Parker 1971 Cherek et al 1973] fish will swim through apertures [Rasa 1971] and mice will bar press [Connor 1974 Connor and Watson 1977] or run in T mazes [Tellegen et al 1969 Legrand 1970 Tellegen and Horn 1972 Kelsey and Cassidy 1976] and obstruction boxes [Lagerspetz 1964] Rats [Dreyer and Church 1970 Taylor 1975] and hamsters [Eibl-Eibesfeldt 1971] will run T mazes for attack opportunities Monkeys will pull a chain to provide themselves with an inanimate target [Azrin et al 1965]

Kelsey and Cassidy [1976] found that mice given a choice in a T maze showed no preference between an accessible target mouse and a mouse behind a wire screen. They argue that the apparent preference for fight interactions observed in their own and other previous studies was unrelated to fighting but actually reflected the rewarding social value of the visual auditory and olfactory cues of the target mice. Taylor [1977] interprets his observation that highly aggressive rats will choose to interact with another highly aggressive rat in preference to a submissive rat 30% of the time as support for the hypothesis that there can be an affiliative component in agonistic interactions. While this is an important theoretical and methodological point the conclusion that social affiliation is necessarily the sole reinforcement present in the fighting situation is not justified by the results. Since Lagerspetz [1964] has suggested that priming is necessary for reinforcement by aggression in mice it is noteworthy that the ICR mice used by Kelsey and Cassidy unlike the several strains tested by Tellegen and Horn [1972] did not show any priming effects on successive trials. Furthermore Kelsey and Cassidy's target mice were not optimal because they could counter attack. Therefore the fighting encounters may have been less than completely rewarding for the aggressive mice. One lesson to be drawn from this work may be that the strong affiliative tendencies of colonial species like the rat make them an inappropriate choice for studies of relatively pure aggression reinforcement. Conversely species which are territorial isolates in the field e.g. the hamster may be more appropriate choices. Although some questions remain the weight of evidence supports the conclusion from the earlier paired encounter studies that under appropriate conditions the performance of intraspecific aggression is positively reinforcing.

Further Comments on the Reinforcing Value of Intraspecific Aggression

Since the animals in these operant conditioning experiments were actively seeking out targets it is clear that they were not fighting in order to remove the presence or interference of another [Craig 1928]. Though in the field such fighting might result in the dispersion of animals which is a presumed adaptive function of intraspecific aggression [Wynn Edwards 1962] this is not a causal

proximal factor in the behavior of individual organisms. In the theoretical views of G. Kohn and Schiff [1968] intraspecific and predatory aggression are performed because this performance has come to be rewarding to the individual through evolution just as many other species typical acts have so evolved. Since attack is a prepotent response under the circumstances of these experiments the reinforcement might also have been predicted from Premack's [1959] principle that the opportunity to perform a behavior which occurs at high rate can be used as a reinforcement for a behavior occurring at a lower rate.

The condition of the positively reinforcing character of intraspecific aggression has been delayed for obvious reasons anecdotal accounts of enthusiastic fighters among humans notwithstanding. In naturalistic encounters the possibility of an attack from the target has made attackers fearful as well as aggressive and the reinforcing effects of aggression have been obscured by the simultaneous presence of fear. Intraspecific attack may contain elements of or alternate with defense (see below). In the laboratory however it is possible to artificially arrange encounters so that the aggressor can be assured of a painless victory and the fear components eliminated through learning. Thus interpretation fits nicely the effects Kahn [1951] obtained using Scott's technique for training young mice. Elimination of fear by a succession of easy wins eradicated automatic components of fear (pilo erection defecation) and of the preflight threat display. Threat is often taken as an indicator of ambivalent motivation e.g. Ewer [1968] and produced rapid repetitive severe and indiscriminate attacks by the trained mice.

A few studies which have explored the characteristics of intraspecific aggression as a reinforcer suggest that it may be weaker than and/or different from more conventional reinforcers. Thus Hogan et al [1970] have found that fighting fish fail to achieve high ratio performance on operant schedules when displaying visual stimuli are used as reinforcers. When compared directly to food reinforcement under similar conditions visual reinforcement also produces lower rates of responding and faster extinction [Hogan et al 1970]. Similar results have been reported with fighting fish by Thompson [1969] and Turnbough and Lloyd [1973] and with fighting cocks by Thompson [1964] although in these latter studies it is unclear whether aggressive displays were actually being elicited. Both Hogan et al [1967] and Thompson [1964] remarked that operant responding for aggression often came in bouts in contrast to the more regular responding found for food reward. This may reflect the natural bout structure grouping of attacks and may account for the failure to acquire high ratio schedule performance. Hogan [1974] and Fantino et al [1972] provided food-deprived fighting fish with simultaneous choices between food and mirror display reward. Hogan found an overall preference for food. Fantino et al reported a preference for display. The differences in results cannot be explained in terms of relative food deprivation.

since Fantino et al's subjects were deprived for longer periods than Hogan's. Another procedural difference may be important however. Fantino et al permitted continuous unrestrained access to both rewards. Hogan followed two free choices by two forced choices of the other reward. If maximum aggressive behavior is dependent on a warm up effect produced by successive displays [Hogan and Roper 1978] then Hogan's procedure would not have yielded maximum aggression because of the interruptions occurring between successive displays. The same may have been true in the Runic's [1977] study. For further review of the relevant studies of aggression in fish see Hogan and Roper [1978].

Among mice Tellegen and Horn [1972] found acquisition of T maze performance for aggression reward slower than that for food reward. Connor and Watson [1977] report that the opportunity for intraspecific attack supported the acquisition of an operant 2 bar discrimination but not its reversal.

These differences between aggression and more conventional reinforcers may reflect the imposition of the temporal properties of aggression on the operant situation. The existence of warm up and satiation effects implies that operant performance may be affected by the subject's immediate prior history of fighting. Evidence for this supposition comes from studies in which a brief priming fight occurring immediately before a trial in a shuttle box [Lagerspetz 1964, Legrad 1970] or a T maze [Tellegen et al 1969, Tellegen and Horn 1972] significantly facilitates operant performance for aggression. This priming effect may reflect general arousal; it may also indicate that the performance of an aggressive response makes the performance of subsequent aggression more reinforcing. This in turn is only one aspect of the difficulty in monitoring and manipulating levels of aggressive motivation. Thus adequate comparisons between the reward value of conventional reinforcers and the opportunity for intraspecific aggression is dependent upon finding solutions to the problem of the experimental control of aggressive motivation.

Reinforcing Value of Defensive (Irritable) Aggression

Aversive stimulation (eg. foot shock) is a well known and widely used experimental provoker of attack. Two of the operant studies cited above [Dreyer and Church 1970, Azrin et al 1965] used shock to provoke attack suggesting that even with painful stimulation attack can be positively reinforcing. However, pain induced aggression obviously occurs in a generally aversive situation. The attacks elicited in this situation may more closely resemble naturally occurring defensive aggression rather than appetitive intraspecific aggression. This implies that the animal would flee rather than attack if given a choice. For example, the upright posture shown by rats in the shock situation was called the fighting posture by Ulrich and Azrin [1962]. However, this posture can be identified with the "upright defense posture" assumed by wild rats [Barnett 1958, Eibl-Eibesfeldt 1969] and by laboratory rats [Grant and Mackintosh 1963] when attacked by a conspecific.

Recent experimental evidence has strengthened this identification for rats [Reynierse 1971 Blanchard et al 1978] although the data for mice are somewhat more ambiguous [Kimbrell 1969 Legrand and Fielder 1973]. It is usually assumed defensive postures indicate fear and/or a preference for flight. These observations lead to the expectation that in rats at least avoidance and escape would be preferred to attack in the shock elicited fighting situation. Studies of the relationship between attack and escape in shock-elicited defense aggression do not at first glance fulfill this expectation. Shock-elicited attack between paired rats occurs with sufficient frequency to retard their acquisition [Azrin et al 1967 Flory and French 1971] and/or performance [Ulrich and Azrin 1964 Ulrich et al 1967 Ulrich 1967 Davis 1969 Logan and Boice 1969] of operant (bar pressing) escape or avoidance of shock. The relative frequency of operant escape and attack depends on experimental conditions [Azrin et al 1967] and the subjects' prior experience [Powell et al 1972]. However, Azrin et al [1967] found that with repeated sessions operant escape eventually becomes prepotent. More generally, our earlier expectations are fulfilled if escape and avoidance response topography are considered. Attack competes with escape when bar pressing is the operant for producing escape; the delay of shock to actual physical escape or flight from the shock chamber is possible and escape becomes totally prepotent over attack [Azrin et al 1967 Logan and Boice 1969 Wolfe et al 1971 Whitman and Doleys 1973]. Similarly, when shock is avoided by freezing in a certain orientation, no fighting occurs [Sbordone 1977]. Thus, when attack and escape (or avoidance) are compared using "primitive" unlearned responses, escape (or avoidance) is prepotent in the shock situation. Attack which has been elicited by aversive stimulation may be somewhat reinforcing perhaps as a way of coping with stress [Weiss et al 1971] but the preferred response is escape from the entire situation. This result perhaps serves as a metaphor, if not a model, of some human aggression which is conscripted into combat.

Reinforcing Value of Intracranially Elicited Aggression

Studies of brain stimulation suggest that the reinforcing properties of different stimuli may be an integral part of the neural circuitry which produces the response. Since aversive peripheral stimulation can elicit attack, it is not surprising that Plotnick et al [1971] found that aversive central stimulation in monkeys also elicits attack. It is important to note, however, that by no means all the stimuli which elicit attack are aversive. Stimulation of which was aversive yielded attack when stimulated [Plotnick et al 1971] but hostility provoking amygdala stimulation was experienced as unpleasant by a human patient [LeDoux et al 1971]. There is also evidence that brain stimulation-elicited attack can be positively reinforced. Nakao [1958] and Fonberg [1967] found that cats and dogs would attack when stimulated in the hypothalamus. The opportunity to escape from hypothalamic stimulation which produced

fear flight reactions but would not escape from rage attack producing stimulation [but see Roberts 1958]. In partial agreement Adams and Flynn [1966] reported that cats would escape from medial hypothalamic stimulation which elicits affective defense but not from lateral hypothalamic predatory attack stimulation. Stimulation of the hypothalamus in the rat has produced the same medial-lateral differentiation found in the cat. Vernges and Karl [1970] found that medial hypothalamic stimulation elicits an affective defensive poorly directed apparently negatively reinforcing attack. Effects of lateral hypothalamic stimulation are mixed but as suggested by Woodworth [1971] may be described as follows. In a posterior region lateral and dorsal to the ventromedial nucleus of the hypothalamus (VMH) stimulation produces a well organized and natural appearing apparently positively reinforcing predatory killing attack [De Sisto and Huston 1971, Woodworth 1971, Panksepp 1971, Vernges and Karl 1969]. Stimulation in a more anterior region ventrolateral to the VMH is more likely to produce an affective apparently negatively reinforcing attack similar to the effects of medial stimulation [Panksepp and Trowell 1969, King and Hoebel 1968, Panksepp 1971].

Other evidence for positive reward value comes from tests of self stimulation at attack producing sites in the brains of monkeys, rats and guinea pigs [Robinson et al. 1969, De Sisto and Huston 1971, Woodworth 1971]. Chaurand et al. [1974] and Martin [1976] have reported that brain loci yielding intraspecific or predatory attack upon stimulation will also support self stimulation. Unfortunately the interpretation of these observations is problematic. Valenstein [1974] has made the entirely justified criticism that the typical operant tests of self stimulation involved quite different temporal and subject control parameters of stimulation than those used to elicit aggressive behaviors. The fact that self stimulation effects are wholly dependent on parameters like pulse duration [Valenstein and Valenstein 1964] and subject control [Steiner et al. 1969] suggests that the definitive tests in which the same stimulation parameters are used both for eliciting aggression and for self stimulation remain to be performed.

Some Speculations on the Reinforcing Value of Aggression Among Humans

If human hunting with weapons is regarded as homologous or analogous to predatory behavior then the existence of sports hunting would suggest a similarity in the reinforcing values of these behaviors. However differences in weapons, time and social circumstances of hunting in different cultures make it difficult to ascribe the reinforcing value to the killing itself. In general the absence of the typical stereotyped behaviors among humans makes it difficult to cite various instances of human aggression. A possible exception to this statement may be the existence of pancultural facial expressions of anger (among other emotions) described by Ekbl-Eibsfeldt [1971] and Ekman [1973]. Perhaps anger may be regarded as the subjectively experienced affect accompanying some form

of intraspecific aggression in humans. Here we must largely rely on subjects' verbal reports of pleasure and displeasure: the correspondence of such verbal reports to the behavioral indicators of reinforcement is as always moot. The latter is regarded as a negative emotion by many psychologists; therefore current reports that at least some individuals show or report pleasure in carrying out a direct and/or overt attack. There have been such comments from or about children [Bovet 1923; Bender et al 1936; Goodenough 1931], farm boys [Eibsfeldt 1974], graduate students [Richardson 1918], athletes [Melles and Harris 1970], psychiatric patients [Hartmann et al 1949; Freud 1972], and soldiers [Gray 1967; Storr 1972; Zimbardo 1969], and nonwestern warriors [Watson 1971]. The persistence of gratuitous cruelty and torture throughout human history has sometimes been explained by its reinforcing value [Storr 1977]. Such pleasurable feeling may not, however, be simply a concomitant of specifically aggressive overt attack. Pleasure may derive from the vigorous physical activity of fighting, the accompanying arousal, or the successful performance of a complex fighting skill. Pleasure may also issue from the fruits of victory: material rewards and social approval of machismo and/or of skill in fighting. Individual processes of self image enhancement and/or of the strengthening of psychodynamic defenses may be equally or more important. For some people, stimuli associated with aggression may become secondary rewards by being conditioned to more primary rewards: certain personality types and past histories predispose to increased attack when pain cues are elicited from the victim [e.g., see Berkowitz 1974; see also Toch 1969, p. 162; Zimbardo 1969; Miller and Caggula 1966; Swart and Berkowitz 1976]. Some of these processes may be reflected in the interest of some individuals in violent spectator sports: ancient gladiatorial contests to contemporary demolition derbys. In other individuals, aggression induced feelings of pleasure may be masked by guilt and social anxiety.

Some combination of these and other processes may account for the extreme ecstatic violence described in anthropological and historical sources: e.g., the joy of the Viking berserkers of Andaman Islanders and of Malaysian Iban and American Indian groups in which fear apparently vanished and the warrior was seized with a feeling akin to joy [Kennedy 1971; Storr 1972; Zimbardo 1969; Dentan 1968]. Extended rituals involving vigorous dancing, singing, and strong social approval if not initiation of aggression [e.g., Wheeler and Caggula 1966] appear to be a necessary preparation or accompaniment in some of these cases. Repetitive provoked violent attack has been reported to lead to similar ecstatic states in contemporary accounts of military violence in Vietnam [Zimbardo 1969] and of civilian violence in Columbia [Leon 1969]. Such reports are reminiscent of the well known phenomenon of *amok* occurring in certain ethnic groups in Malaysia, Indonesia, and the Philippines [Schmidt 1977; Burton Bradley 1969]. In fact the historical allusions to *amok* suggest

that a century or more ago *amok* may have been similar to the instances described above: a state of high aggressive motivation induced through social contention as a preliminary to pirate raids [Galloway 1923] or to warfare [Murphy 1973]. In the course of time the nature of *amok* has evidently changed. The current consensus appears to be that contemporary *amok* is a 4 part syndrome afflicting individuals in whom an acute or chronic social stress produces a period of withdrawal followed sooner or later by a relentlessly homicidal outburst. Survivors of their own *amok* episodes claim amnesia for the event. Phenomena resembling *amok* in some of these respects although with a lower probability of homicide have been reported among the natives of Tierra del Fuego [Comar 1915], Kenya [Carothers 1948] and of New Guinea [Langness 1965, Lowman, Vayda 1971].

There seems to be some resemblance between the current form of *amok* and ecstatic violence including a narrowing of the perceptual field and a disregard for personal safety [Schmidt et al 1977] during attack. On the other hand Van Loon's [1927] old account presumably based on interviews with *amok* survivors suggests that *amok* is a subjectively terrifying rather than euphoric experience. This is consistent with reports of paranoid ideation in *amok* survivors [Schmidt et al 1977]. While historically *amok* may have been related to the deliberately induced aggressive motivation of ecstatic violence, currently *amok* appears to be a culturally sanctioned response to stressful social situations.

Some psychiatrists have suggested that ecstatic violence may be similar or equivalent to sexual pleasure and orgasm [Novick and Novick 1972, Miller and Looney 1974, Fornari 1975]. Although it has been found that strongly but not weakly erotic stimuli can nonspecifically facilitate aggression [Donnerstein et al 1975, Zillman and Sapolsky 1977], the biological origins of ecstatic violence should probably be sought in the reinforcing value of aggression, not sex. In special circumstances in which social prohibitions and internal inhibitions (e.g., aggression anxiety) are weakened, a response which is intrinsically reinforcing and which facilitates its own motivation must produce a positive feedback of the kind observed in ecstatic violence. Ecstatic violence may be the human equivalent of the warm up and priming effects seen in other animals. According to this hypothesis, cultural sanctions determine the circumstances of the attack, the weapons selected, and the victims initially chosen. Once the attack is set in motion, intrinsic biological mechanisms become more important in determining the ultimate outcome [Zimbardo 1969].

The form of extreme overtly homicidal aggression experienced personally by the largest number of people is war. Most soldiers are conscripted under such conditions of low aggressive motivation and realistic evaluation of danger that the most commonly reported emotion in battle, as in the laboratory experiment, is

in nonhuman animals described above special circumstances must occur to unmask the positive reward value if any of aggression. Certainly easy killing [Balle] does seem to generate in human beings symptoms of pleasure [Keeton 1976 p. 278]. The development of high aggressive motivation which sometimes far can apparently have a similar effect. The weight of the evidence suggests that overtly homicidal aggression becomes strongly positively reinforcing for the majority of humans only under special conditions of high aggressive motivation and low inhibition.

Implications for Theories of Aggressive Behavior

This paper began with a description of some of the temporal patterns involved in aggression. The succeeding sections reviewed the evidence for the positively reinforcing value of predatory and intraspecific aggression under the appropriate conditions. In this last section I present the hypothesis that these two sets of observations are related. Other things being equal temporal fluctuations in attack rate are a consequence of fluctuations in the reinforcing value of aggression. Warm up and priming effects reflect an initial transient increase in the reinforcing value of aggression; refractory periods and satiation effects reflect a longer term decrease. This hypothesis is generally in keeping with contemporary notions of incentive motivation according to which reinforcers pull responses more than they push them (eg Bindra 1974). The specific model for this hypothesis is the work of Cabanac [1971] who in a series of elegant experiments has shown that the hedonic value of a stimulus (eg a pulse of heat or a taste of sugar) is dependent upon the state of the subject (skin temperature or sugar load). In the context of aggressive behavior the term aggressive states (AS) seems appropriate. The aggressive states are those sets of internal conditions which vary among other things the reinforcing value of an overt attack. In conjunction with a variety of other internal and external conditions (eg stimulus situation, learning history) they determine moment to moment attack probability. The subjective experience of anger in humans may reflect a conscious concomitant of AS. Hopefully AS can eventually be linked to definable sets of neural and hormonal mechanisms.

The fact that both warm up and satiation effects are induced by prior aggression implies that there must be multiple feedback connections between AS and overt aggression. Thus the occurrence of warm up effects implies the existence of a positive feedback link between overt attack and AS. Conversely rate short term and long term negative feedback relationships between overt attack and AS can account for refractory period and satiation effects respectively. A detailed discussion of these feedback mechanisms is beyond the scope of this

paper. The important point for the present is that when environmental variables are adequately controlled, temporal fluctuations in aggressive behavior may be viewed as manifestations of changes in the underlying AS.

On this hypothesis, it is obvious that changes in AS indicated by temporal fluctuations of overt aggression must necessarily have a profound effect in the operant experiments described above. More generally, although the positive reinforcing value of aggression particularly in humans may become substantial only under special conditions, this phenomenon must be reckoned with in any general theory of aggressive behavior.

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Modulation of Aggression Toward an Intruder During the Reproductive Cycle of White King Pigeons (*Columba livia*)

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For three of four mated male pigeons, intrusion of a still, two-dimensional image of a conspecific into the reproductive situation initiated aggressive behavior over months of daily testing with little habituation. There was a transient increase in aggressive contacts against the head of the target within two days prior to or following the occurrence of the second egg. Such an increase did not occur with extended daily testing of the male alone and was more closely synchronized to egg laying than time since the introduction of the female. The results are consistent with previous studies of reproductive and schedule induced aggression in birds.

Key words: aggression, reproduction, pigeon, conspecific target, incubation, intruder, incubatory disruption

INTRODUCTION

Cohen et al. [1979] reported that the head of a conspecific target selectively controls aggression induced by an intermittent food schedule in pigeons. On the basis of their findings and similar results from studies of reproductive aggression toward an intruder, they proposed that schedule induced and reproductive aggression in pigeons may be closely related. Specifically, they suggested that for all birds, possibly other birds, there may be a common perceptual basis for aggressively identifying an opponent in aggression inducing situations. The aggressive

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pigeon may only attend to a specific visual feature(s) of its opponent. To assess the generality of the selective target control of schedule induced attack in pigeons and other possible similarities between schedule induced and reproductive aggression in that species it is first necessary to establish that the conspecific target image used in prior schedule studies [e.g. Cohen et al. 1979, Looney et al. 1976] will initiate aggression when intruded into the pigeon's reproductive cycle and that the aggressive behavior toward it is systematically related to the phase of reproduction.

Studies of avian reproductive aggression toward an intruder have provided measures of aggressive behavior toward some animate and inanimate targets but not on a daily basis throughout the cycle. In Smith and Hosking's [1955] studies of passerines for example a pictorial image of an intruder was not attacked at all during the reproductive cycle. Similarly Vowles and Harwood [1966] studying ring doves and more recently Spurr [1974] studying Adeline penguins encountered difficulties in obtaining daily measures of reproductive aggression toward animate and inanimate targets. The experiments summarized below examine daily fluctuations in the White King pigeon's aggressive behavior against an intruded conspecific target image that previously was shown to be effective in initiating schedule induced aggression.

GENERAL METHOD

Subjects

The subjects were four mated pairs of White King pigeons (P345, P346, P347, P348) that had at least one prior breeding experience at Palmetto Pigeon Plant (Sumter, SC) before arrival in the laboratory. In the laboratory colony room they were housed in individual 39 X 52 X 30 cm cages maintained under controlled lighting conditions (lights on 0700–2100 hr) and given free access to food and water.

Apparatus

Two breeding chambers were located in a room separate from the colony room. Each chamber was a modified steel dog cage (73.7 X 106.7 X 66.0 cm) with the front (73.7 X 66.0 cm) replaced by wire mesh to allow video monitoring by a QSI (Model Q5000) low light video camera. As shown in Figure 1 a nest box (33 cm in diameter) was located in one corner formed by the mesh screen and side wall. On the side wall 20 cm from that corner (center of screen to corner) was a 11.5 X 15.3 cm rear projection screen [Cohen et al. 1976] suspended by four switches so that screen contacts could be recorded. The bottom of the screen was 7 cm above the floor and a projector [Cohen et al. 1976] was mounted behind the screen. Centered on the side wall opposite the screen were dispensers for nest material (pine needles), food and water. A 15 watt daylight fluorescent bulb mounted on the ceiling of the chamber provided the same lighting conditions

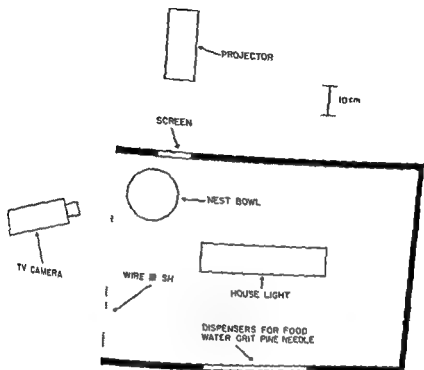


Fig 1 Overhead view of breeding chamber

used in the colony room. A fan provided ventilation and masking noise. The target stimulus was a rear projected full view colored image of a male White King pigeon (intact target) [Cohen et al 1979] that was unfamiliar to the experimental birds and is effective in releasing schedule induced aggression. Solid state equipment and counters were used to schedule experimental conditions and record target contacts from an adjacent room.

Preliminary Breeding Procedure

After a minimum of four weeks in visual isolation each pair was placed in the breeding chamber with free access to food water grit and nest material. They remained there for seven to ten days after the occurrence of the second of two copulations for a total of 12-17 days. Each pair was given this preliminary breeding experience either one or two times separated by a minimum of two weeks in isolation. The male was marked with a black dot on the tail for easy visual identification. During breeding the temporal sequence of pre incubatory behavior (court

ship copulation nest building and demonstration and laying of two eggs spaced 24–36 hours apart) and incubatory behavior of the White King pigeons [Levi 1974] was comparable to that of other pigeons and doves as described by Fabricius and Jansson [1963] Lovari and Hutchinson [1975] and Miller and Miller [1958]

Target Intrusion Procedure

During testing alternation of breeding in the test chamber with two weeks of visual isolation in the colony room continued with the addition of daily intrusions of the conspecific image into the breeding chamber. Although several different methods of intruding the target during a daily test session were used (as described below) the general testing procedure was as follows. A pair of birds was placed in the chamber at approximately 1600 hr and daily testing was begun the next morning. During testing the fluorescent chamber light was turned off for the duration of the target presentation (5 or 15 min/day) to ensure a clear image and to obtain stimulus conditions similar to those used in schedule induced aggression studies [Looney et al 1976 Cohen et al 1979]. During most test sessions the pigeons' behavior in the area of the nest bowl and screen was video monitored. Video recordings were made periodically. Test sessions were conducted at 0900 hr seven days/week except when precluded by equipment difficulties. During breeding birds remained in the chamber until after hatching of the squab or abandonment of the eggs. In Experiments 1, 2, and 3 if the birds did not incubate the eggs for two consecutive days or if one or both eggs were broken testing was terminated and birds returned to the colony room for at least two weeks.

Pilot experiments with ad libitum food indicated that the male of the mated pair initially exhibited aggressive behavior (pecking, charging, bow-coo) toward the conspecific image. However, attack habituated after several target presentations within one test session. In addition, both the male and female manipulated food spilling and distributing it around the chamber (false feeding) [Murton et al 1969]. These observations, together with prior reports [Azrin et al 1966, Dove 1976] that restricted food intake facilitates aggressive behavior suggested that free access to food was not a suitable condition for obtaining sustained reproductive aggressive behavior against a two dimensional conspecific image. Consequently in all of the following experiments access to food was reduced from ad libitum to one hour/day (1200–1300) such that the birds were deprived of food for 20 hours at the time of testing (0900 hr). Birds were maintained on the same restricted food schedule during isolation.

EXPERIMENT 1

During the initial experiment two pairs of birds were given repeated exposures to the conspecific image during each day of the reproductive cycle.

346 and 347 were used. Each daily session consisted of ten 90 second presentations of the target for a total presentation time of 15 minutes/day. Five seconds elapsed between target presentations. The number and temporal distribution of contacts on the projection screen with and without the target turned on were recorded for each one hour session.

and Discussion

Video monitoring and periodic video tape recording of test sessions indicated that only the males of the mated pairs exhibited aggressive contact (chasing and pecking at the head) and noncontact (guttural vocalization, bowing) behavior toward the intruded conspecific image. Virtually no behavior occurred on the screen when the target image was turned off. When the target image was turned on, the female left the vicinity of the target and nest regardless of whether she was incubating the eggs.

Figure 2 summarizes daily fluctuations in aggressive contact (contact/min on the screen) toward the intruded conspecific image during the reproductive cycle as a function of successive breeding days, with arrows indicating the occurrence of the eggs during incubation of the squab. P346 and P347 incubated eggs during initial breeding cycles in the absence of the target. However, the initial two attempts to breed P347 with the target intruded resulted in their abandoning and breaking their eggs within two days of laying. Available data from those initial cycles for P347 were consistent with the results of the third, more successful attempt in which the pair incubated their eggs for 11 days following laying of the second egg. The results for the third breeding attempt with the target intruded are presented in Figure 2.

For the males of both pairs, there was a three- to fourfold increase in attack rate toward the intruded conspecific image prior to or following the occurrence of the second egg and a subsequent decrease in rate of attack to approximately preincubatory levels within two days prior to or following the occurrence of the second egg without a further change in level of aggressive behavior, whereas P346 hatched on the eighteenth day following the second egg was accompanied by a second increase in attack rate. Although the breeding cycle for P347 was disrupted, males of both pairs showed a transient increase in aggressive contacts toward the intruded conspecific image at the time of egg laying.

EXPERIMENT 2

Video monitoring of incubatory behavior in Experiment 1 indicated that the eggs were temporarily abandoned for the duration of the target presentations. The male was disturbed and pecked at the conspecific image and the female left the immediate vicinity of the nest. Stout and Brass (1969) reported a similar disruption of incubation by the intrusion of a conspecific model into the nesting area of gulls. In an

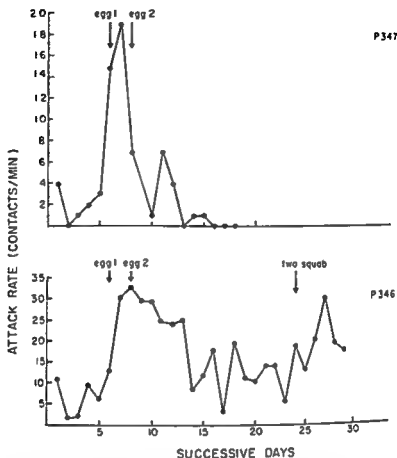


Fig. 2. Attack rate (contacts/min) on the projected image as a function of successive breeding days. Day 1 corresponds to the first complete day of testing. Note that the ordinate scales for the upper and lower panels are different. The arrows indicate the occurrence of the first and second eggs and, in the case of P346, of hatching of squab.

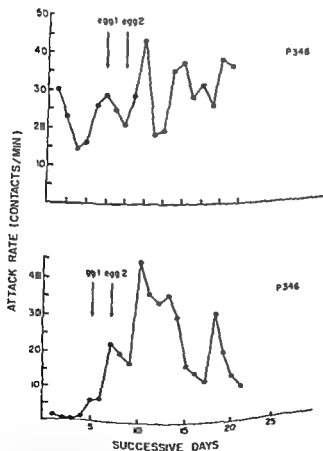
effort to reduce the disruption of incubatory behavior and prolong the reproductive cycle, the duration and number of target presentations was reduced in the next experiment.

Method

Mated pairs 345, 346, and 348 were used. The procedure was the same as that used in Experiment 1, except that there was one five-minute target presentation per session instead of ten 90-second target presentations. Number of contacts on the projection screen was recorded for five minutes preceding, during, and for five minutes following presentation of the conspecific image.

Results and Discussion

Figure 3 summarizes daily fluctuations in the male's aggressive behavior toward the intruded conspecific image for the portion of the reproductive cycle completed by P346 and P348. With the reduced exposure to the conspecific image in this experiment P346 that successfully bred in Experiment 1 and P348 abandoned their eggs midway through the incubatory period (days 19 and 21 respectively). Both pairs showed a transient increase in aggressive behavior at egg laying. The results for P345 are not included since the male of that pair failed to exhibit sustained aggressive behavior toward the intruded image. Unlike the other two P346 and P348 completed the reproductive cycle through hatching of the squab in spite of the daily intrusions of the conspecific image.



Attack rate (contacts/min) on the projected image as function of successive days. Day 1 corresponds to the first complete day of testing. The arrows indicate the days of egg laying.

As was the case in Experiment 1, an increase in attack rate occurred with days prior to or following the occurrence of the second egg. Whereas attack subsequently decreased for P346, there was less of a decrement for P348. Representative event records of aggressive contacts on the screen before, during, and following image presentation are presented in Figure 4. Both males initiated at target onset. For P346, attacks occurred primarily during the initial two to three minutes, whereas for P348, attacks continued until target termination, occasionally running over into the target off condition.

EXPERIMENT 3

The sustained rates of attack and repeated temporal contiguity of attack at target termination (Fig. 4) for the male of P348 suggested that target termination or onset of the chamber light may have adventitiously reinforced [Skinner 1957, Azrin and Hutchinson 1967] target responses. Since reinforcement of attack could mask daily changes in aggressive behavior related to the phase of the reproductive cycle, the testing procedure in Experiment 3 was modified so that target termination and light onset were not immediately preceded by a target contact. In addition, to assess daily fluctuations in aggressive behavior in a nonreproductive situation, the male was exposed to daily test sessions in the breeding chamber with and without his mate available.

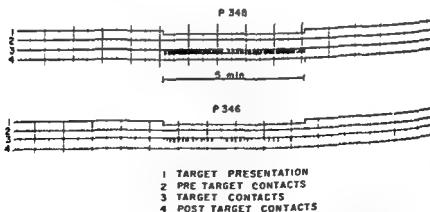


Fig. 4. A representative event record of aggressive contacts on the screen before, during, and following a single five minute presentation of the conspecific image for P346 and P348.

Method

Following Experiment 2 the females of pairs P346 and P348 eggs and used nest materials were removed from the test chambers. Each male remained in the chamber alone and was exposed to the testing procedure for ten daily sessions. This was followed by the reintroduction of the female with continued daily testing. The procedure was the same as that used in Experiment 2 except that a protective enclosure ensured that target termination and light onset were not immediately followed by a target contact. If a target response occurred during the final ten seconds of the scheduled five minute image presentation the image remained on and the lights off. If no contacts occurred for an additional ten seconds upon completion or termination of the reproductive cycle the female eggs and nest material were again removed and the male alone was tested for 10 (P348) or 27 (P346) days. The breeding (♂ ♀) condition was then repeated for both pairs. Finally the males of P348 and P346 were left alone for 12 and four days respectively.

Results and Discussion

Figure 5 summarizes daily fluctuations in the males' aggressive behavior (attacks/min) toward the intruded conspecific image for successive breeding and nonbreeding (♂) conditions. As in Experiment 2 both pairs of birds abandoned their eggs midway (5-7 days following the second egg) through the incubation period. Introduction of the female initially suppressed attack against the intruded image for P346 and to a lesser degree for P348. With the exception of day (57) for P346 attack rate was less than 20 contacts/min during the incubatory periods for both birds and was followed by a twofold increase in attack rate within two days prior to or following the occurrence of the second egg. Subsequent decrease in attack rate during the incubation period for both birds in this experiment suggests that adventitious reinforcement by target termination and chamber light onset contributed to the sustained high rates of contact observed following egg laying for P348 in Experiment 2. For both pairs removal of the female had no systematic effect upon the males' attack rate. In addition extended daily testing (25-27 days) between breeding cycles the males showed no evidence of transient increase in attack rate like that observed at the time of egg laying during the breeding cycle although attack rates gradually increased over successive days for P346 and decreased for P348.

Discussion

Three of four male White King pigeons on a restricted food schedule initiated a three of four male White King pigeons on a restricted food schedule initiation of a nonmoving two-dimensional image of a conspecific into the reproductive cycle was sufficient to initiate attack over as many as seven months of testing with little habituation. The same visual image of a conspecific also

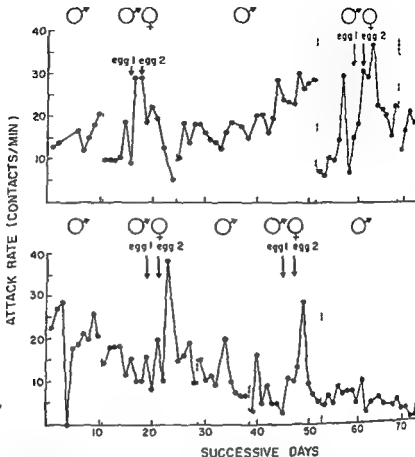


Fig. 5. Attack rate (contacts/min) on the projected image as a function of successive (d) breeding and nonbreeding (d) days. The arrows indicate the occurrence of the first and second egg laying during breeding.

effective in maintaining schedule induced aggression over months of daily exposure to the same species. Since only the one conspecific image was used in the experiment, it is unclear whether aggression toward it was selectively controlled by the conspecific target's head as it is with schedule induced aggression [Cohen, 1979]. Audiovisual monitoring, however, suggests that attack was controlled by the head, since aggressive pecks were directed at that region of the conspecific image. Perhaps intermittent intrusion of other visual stimuli such as an intruder, a bird of a sympatric species, a predator, or even an inanimate stimulus could be sufficient to initiate aggression. Additional research is needed to provide a detailed description of the aggressive motor patterns and vocalizations directed toward the intruded stimuli as well as the specificity of visual target control of that behavior during the reproductive cycle.

Present experiments demonstrate the feasibility of studying the daily course of aggression toward an intruded stimulus in the reproductive context. A general procedure indicated that the sustained level of aggression against a two-dimensional image in the present experiments was related to the restricted schedule. This is consistent with failures to obtain sustained aggression toward an intruder in prior studies in which food was not explicitly restricted (Hinde and Hoshino, 1955; Vowles and Harwood, 1966) as well as Hinde's (1970) notion that changes in internal state can influence the relevance of the stimulus.

As reported in studies of reproductive aggression in birds (Smith and Hinde, 1955; Vowles and Harwood, 1966; Spurr, 1974), the male in these experiments was more aggressive toward the intruder than the female and the level of aggressiveness toward the intruded image varied considerably between birds. In the present experiment, differences in rate of aggressive contact, the three of four subjects that exhibited sustained aggressive behavior against the intruded image, showed a transient increase in rate of target contact within two days of the laying of the second egg. The form and time course of that increase is similar to that obtained with ring-necked doves [Vowles and Harwood, 1966] using a group of four to six days following the occurrence of the first egg. Spurr (1974) reported an increase in aggressiveness after egg laying in Adelie penguins, although in that study aggressive behavior did not reach a peak until the time of egg hatching. The peak in aggressiveness in this study is closer to the time of egg laying than in the experiments with other species, which may be related to the differences in species' experimental conditions (daily testing, targets, etc.) and to the factors responsible for the transient increase in the male's aggressiveness toward an intruder following egg laying are unclear. Recent studies with ring-necked doves (Silver et al., 1974; Feder et al., 1977; Silver, 1978) suggest that changes in the levels of progesterone, testosterone, and prolactin at the time of egg laying are not responsible for this increase. Similarly, the decrease in the male's aggressiveness toward the intruder following the introduction of the female (Experiment 3) shows that any major change in the male's external environment is necessarily accompanied by enhanced attack on the intruded image. The results of Experiment 3 indicate that the increase in aggressiveness at egg laying is due to extended daily testing of the male alone and is closely synchronized with egg laying and not to the amount of time elapsed since the introduction of the intruded image. It is likely that the transient increase in the male's aggressiveness toward the intruded image at egg laying is related to the external stimulation (visual and auditory-olfactory) that accompanies the onset of incubation.

With the exception of the first breeding cycle for P346 (Experiment 1) all three pairs of birds that exhibited sustained aggression toward the intruded conspecific image also abandoned or broke their eggs midway through the incubation period. Although the cause of this incubatory disruption is unknown we have evidence that it is not due to the restricted food schedule. Subsequent breeding of all pairs without daily intrusion of the target was successful through hatching in spite of the restricted food schedule. In addition the pair (P345) that failed to exhibit sustained aggressive behavior against the conspecific image (Experiment 2) completed the breeding cycle through hatching. An alternative explanation of the incubatory disruptions is that the agonistic behavior that accompanies repeated forced intrusion of a novel conspecific image into the breeding area is sufficient to disrupt or block incubation. The fact that the birds that showed the disruptive effect left the nest and engaged in agonistic behavior during the target presentation is consistent with this view. Although this interpretation is appealing in view of similar disruptive effects reported in field studies with birds [Lack 1955; Smith and Hosking 1955] additional experiments are needed to determine if disruption of incubation in the present situation was specific to intrusions of a visual image of a conspecific.

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Brain Damage in Infant and Adult Rats: Effects on Activity, Emotionality, and Muricide

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Septal lesions produced signs of increased emotionality in the adult rat: the "agitated" syndrome (hyperresponsiveness to handling in the open field, decreased feeding and ambulation activity, increased defecation, deficient habituation) was more or less complete and more or less marked depending on the age at which the lesion was performed (7 days or 3 months), the extent of the lesion (restricted to the septum or extending to more ventrally located structures), and the environmental conditions in which the animals were reared (in groups or in isolation). All septal lesions provoked a similar and significant increase in the probability of occurrence of mouse-killing behavior, irrespective of age, sex, extent of lesion, and kind of rearing environment. In a 24-hour experiment starting at 11:30 a.m., the rats septalectomized at adult age were more active than controls during the initial period, while all septals were significantly more active than controls during the night period. Early septal lesions only transiently disrupted weight gain. The results obtained point to complex interactions between the effects of early brain damage and environmental conditions.

Key words: septum, ontogeny, emotionality, mouse killing behavior, open field

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INTRODUCTION

The rat's mouse killing behavior has been investigated by our group for more than 20 years since the original descriptive study dealing with this interspecific aggression [Karli 1956]. The general perspective of our investigations inevitably changed over the years. In a first stage, both lesion and stimulation experiments were carried out in order to draw up an inventory of the brain mechanisms which were thought to rather specifically facilitate or inhibit the release of the killing response [Karli et al 1969]. Later on, more emphasis was laid on the intimate relations which exist between emotional reactions and responses in the ontogenesis of behavior and in the behavior of the adult organism [Karli et al 1974]. More recently, the fact that a brain lesion may have different effects depending on whether the rat has had experience with mice prior to the operation led us to stress the role played by experimental factors to uncover the essential part taken by the amygdala in mediating their influence upon behavioral ontogeny [Karli et al 1977]. The study reported in the present paper cumulatively reflects these closely related preoccupations.

When trying to increase the rat's emotionality in order to find out whether the alteration thus induced would facilitate the initiation of mouse killing behavior, one is obviously led to consider the behavioral effects of septal damage. Destruction of the septal forebrain was indeed shown by a number of investigators to result in alterations often designated as "septal hyperreactivity" or "septal rage" that range from an increased responsiveness to tactile stimulation up to violent flight and attack reactions [Albert et al 1975, 1976; Brady et al 1953, 1955; Dominguez et al 1969; Douglas et al 1966; Fulton et al 1979; Gage et al 1978a, 1978b; Harrison et al 1957; King 1958, 1959; King et al 1958; Nielson et al 1965; Olton et al 1974; Philippis et al 1972; Reynolds 1965; Schinurr 1972; Seggie 1968; Singh 1969; Yutzev et al 1964]. Several experiments, however, failed to produce such a septal rage consistently in rats [Burkett et al 1966; Clody et al 1969; Fried 1969; Knechtlaus et al 1964; Thomas et al 1959; Thomas et al 1972], as well as in cats [Bond et al 1957; Kling et al 1960; McCleary 1966; Moore 1964].

With regard to the initiation of muricide behavior, the results reported are even more conflicting, at least at first sight. Karli [1960] and Malik [1970] found no increase in mouse killing behavior following septal lesions, while Siegel et al [1969], as well as Muzek et al [1972], clearly demonstrated initiation of such behavior in septal lesioned rats. This discrepancy could not be due to strain differences, since Latham et al [1974] found an increase in mouse killing following septal damage in rats of the strain (Long Evans) used by Malik, while they found no change in rats of the strain (Sprague Dawley) used by Muzek et al. But other factors must be taken into account, namely degree of prior experience with mice, site and extent of lesion, and moment of postoperative testing.

It is highly probable that the lack of initiation of interspecies aggression following septal lesions reported by one of us [Karl 1960] was due to the fact that the lesioned rats had been given prolonged experience with mice prior to the operation and that they had thus become familiarized with the presence of a mouse in their cage. Indeed Vergnes et al [1976] showed in our laboratory that on the day following the septal lesion 60% of the rats would kill the very first mouse they were ever presented with whereas no more than 8% of those rats that had been given preoperative experience with mice would display the killing behavior.

That site and extent of the produced lesion also play an important role is clearly illustrated by the results recently reported by Wallace et al [1978]. In their study no effect on muricide was found following either damage restricted to the septum or damage restricted to structures ventral to the septum. Only when the septal damage invaded more ventrally located structures did they observe an increase in muricide. It is worth adding that killer rats were found to be significantly more irritable than nonkillers.

The lesion induced hyperreactivity is known to lessen in progress of time when produced in the adult animal; the septal syndrome is but a transient condition. Even though it may persist for postoperative periods of up to 75 days [Knecht et al 1964] it vanishes quite rapidly (in 5-14 days) if the lesioned animals are handled regularly [Brady et al 1955; Reynolds 1965]. According to Gotsick et al [1972] the dissipation of the septal syndrome depends on the distribution rather than on the amount of handling. With regard to muricide the data obtained by Miculik et al [1972] suggest that there is a close correlation between the lesion induced hyperreactivity and the initiation of mouse killing behavior. Not only was the interspecies aggression displayed immediately following

the lesion of an affective kind but this lesion effect was also a transient one and its time course paralleled more or less that of the septal rage syndrome. One of the rats that were first retested 15 days after surgery (1 when the non-lesioned rats that were first retested 15 days after surgery (1 when the lesion induced hyperemotionality had sharply declined) killed any mouse.

In a recent paper dealing with behavioral effects of amygdaloid lesions performed in both infant and adult rats [Eclancher et al 1979] we recall the fact that even though much sparing of function has generally been observed following early damage to cortical structures substantially less sparing has generally been reported following early damage to brain structures below the cortical level. In the study mentioned early amygdaloid lesions (performed at 7 days or at 25 days) provoked a lasting hyperreactivity together with an increased probability of occurrence of muricide while amygdaloid lesions performed at adult age had no such effect. With regard to the effects of early septal damage our data confirm the rat's general responsiveness have been reported [Endroczi et al 1969; Johanson 1972; Janzen et al 1976; Molino 1975; Phillips et al 1973; Phillips et al 1972; Schoenfeld et al 1974; Stewart et al 1977] but to our knowledge no study has ever considered the question from

the point of view of muricide behavior. Furthermore, little is known about the possible influence of environmental factors upon behavioral ontogeny following early brain damage.

The present study was thus undertaken with the aim of clarifying the following questions:

a. What are the effects of septal lesions with regard to both the rat's reactivity when facing an unfamiliar situation such as an open field and the probability of initiation of muricide behavior according as the septal damage was produced in infancy (at the age of 7 days) or at adult age (at the age of 3 months)? In order to detect possible differential effects of early septal lesions, the animals' reactivity before and after puberty, a first open field test was run at the age of 40 days. Furthermore, the spontaneous activity was recorded by means of an actograph in all septal lesioned animals in order to overcome some of the difficulties usually encountered when trying to interpret the rat's behavior in the open field.

b. When produced through early damage, do the behavior changes depend on size and extent of the septal lesion in the way they do when produced by damage carried out at adult age?

c. To what extent do the behavioral effects of an early septal lesion depend on the environmental conditions in which the lesioned animals are being raised from weaning (either in groups or in social isolation)?

d. What are the lesion-induced effects, if any, on body weight in the adult animal as well as on weight gain in the young animal? Since the possibility can never be ruled out that an observed behavior alteration might be due to a general defective condition, it was of interest to regularly examine body weight and food intake. In addition, the weight of the testes and that of the adrenals were checked in each animal at the end of the experiment.

METHODS

Subjects

Data for this study were collected from 255 male albino Wistar rats taken from litters born in our laboratory. At three days of age, the pups were sexed on the basis of the anogenital space, and the litters were culled so as not to exceed 5-8 male pups per litter. The split litter technique was used in selecting animals for the septal and control groups. Half of the pups in each litter underwent a septal lesion; the other half underwent a sham lesion (control animals).

Surgery and Histology

Septal lesions were produced in rat pups weighing 11-15 gm at the age of 7 days. The surgery was performed under sodium pentobarbital (Nembutal).

anesthesia (0.72 ml/10 gm) administered intraperitoneally using a La Précision Crématoraphique stereotaxic instrument. After incision of the scalp a 1 mm trephine was used to drill a hole in the cartilaginous skull. An electrode insulated with epoxyite except for 0.5 mm at the tip was lowered at points specified in Table I. The circuit was completed by connecting ear bars to the anode. The lesion was produced by passing a 2 mA current for 10 sec at each point. Sulfapowder was applied to the incision before suturing. The ear of each animal was checked for identification and the rat pups were put back to the nest and were left there until weaning on postnatal day 25. At this age the lesioned rats were housed either individually or in groups of three or five rats per cage until 3 months old. The same procedure was employed for the control animals except that no current was passed.

The animals that were assigned to undergo a septal lesion at adult age were weaned at 25 days of age and raised in groups until 2.5 months old. Surgery on these adult animals was performed at 3 months with Nembutal anesthesia (40 mg/kg IP). Stereotaxic coordinates are reported in Table I.

A pilot study had been carried out prior to the actual experiments in order to determine the coordinates that would allow us to produce a complete destruction of the septum in the 7 day old rat pups and also those that would allow us to produce lesions additionally invading more centrally located structures (Table I).

At the end of the study all animals were killed by means of a lethal dose of Nembutal. The brains were removed, stored in 10% formalin for several days, embedded in paraffin and sectioned at 20 μ . Every fifth section was mounted on a slide and stained with cresyl violet. Both adrenals and testes were removed and fully freed of connective tissue and fat then weighed.

General Procedure

All animals were weighed on the day of weaning and once weekly thereafter until termination of the experiment. Animals that had been submitted to early septal lesions (at 7 days) as well as animals that were to be lesioned at adult age were tested in an open field at 40 days of age, three days running.

At 3 months of age those early lesioned and sham operated rats that had been grouped from weaning were housed in individual cages and rats that had been housed in isolation were put in another individual cage. Three days after this change of home cage a mouse was introduced into the rat's cage during the light portion of the light-dark cycle. Twenty-four hours later either the mouse or its position of the light-dark cycle. The rat had never been previously in contact with a mouse. Each rat was retested for its muricidal behavior once a week.

Rats assigned to be lesioned at adult age were grouped from weaning until 5 months. At this age they were housed individually and three days later they were tested in the open field on three successive days. Surgery on these adult animals was performed at 3 months of age. One day after surgery they were

TABLE I Lesion Coordinates and Current Parameters for Septal Lesions in Infant and Adult Rats

Age	Lesion	Anterior to lambda (mm)	Lateral to lambda on either side (mm)	Below skull surface at the λ (mm)	Cathodal current	
					Intensity (mA)	Duration (sec)
7 days	Septum	5	0.3	5	2	10
		4.7	0.3	4.5	2	10
	Septum + ventral structures	5	0.3	5	2	15
		4.7	0.3	5.1	2	10
3 months	Septum	9.5	0.6	5	2	20
		9	0.6	6	2	20
		8.5	0.6	5.5	2	20
				5.5	2	20
				6	2	20

presented for the first time with a mouse and three days later the rats were again tested in the open field.

During the fifth month after birth the food intake of each rat was controlled for three weeks. At about 5 months of age spontaneous activity of all rats was measured for 24 hours in an actograph. After that the animals were submitted to avoidance conditioning (Eclancher et al. in preparation).

Apparatus

Open field. The apparatus consisted of a transparent surrounding wall of Plexiglas (120 X 100 X 30 cm) lying on a white sheet subdivided into thirty 20 squares. A lighting of 1 000 lux in the center of the open field and of 600-800 lux on the edges was provided by lamps placed above the field. Animals were always dropped in a corner of the open field. During the three minutes of test the path covered by the animal was reproduced on a diagram exhibiting a floor of the field reduced to one tenth. From this reproduction of the path followed by the rat locomotor activity was measured by means of a curvometer. The number of rearings and the number of fecal boluses dropped during the three minute observation period were also recorded.

Actography. Spontaneous locomotor activity was measured by placing the rat in an Animex apparatus (Farad Electronics, Stockholm) for a period of 24 hours starting at 11 30 AM. The principle consisted in the recording of changes induced by the animal's movements in an electromagnetic field: these changes induced impulses that were summed up every ten minutes.

Analysis

A two way analysis of variance for unequal numbers was applied to all data. Individual comparisons were made with the Scheffe test only after the overall analysis provided evidence of statistically significant between group differences. In regard to open field data an analysis of variance was performed on locomotor activity, number of rearings and defecation scores as a function of the lesion (restricted to the septum or extending more ventally or sham lesion) of the environment in which the rats had been maintained from weaning and also of the age at which the rats had been lesioned. When a significant main effect was revealed differences in means were evaluated with the Scheffe test. The data concerning activity measured in the actograph (means of the 24 hour activity and means of the activity hour by hour) were submitted to an analysis of variance with lesion, age of operation and postoperative environment as the three factors. An analysis of variance was performed on the means of body weight as well as the means of food intake. When analyzing the percentage of rats the chi square test (with Yates's correction when necessary) was used to compare the different groups.

RESULTS

Histology

Of the 110 rats septalectomized at 7 days of age and assigned to be group reared (lesions restricted to the septum in 50 rats and larger lesions spreading to ventral structures in the 60 others) 64 died during the two weeks following the surgery. In the 46 rats that survived and reached adult age having been raised in groups from weaning, histology revealed eventually that a) three rats had to be discarded because the septum was not entirely destroyed b) 18 rats had undergone a complete destruction of the septum including medial and lateral septal nuclei (group 7 SG Fig. 1a) c) 25 rats had undergone a larger lesion of the type shown in Figure 1b. Structures involved were the lateral and medial septal nuclei the nucleus accumbens septi the diagonal bands the anterior commissure the columns of the fornix the nucleus triangularis septi and in some cases the superior part of the area preoptica medialis (group 7 S+G).

Of the 60 rats septalectomized at 7 days of age and assigned to be isolation reared 21 rats died before reaching the weaning age 10 rats died in the isolation cage 4 rats had to be discarded because of incomplete lesions 25 rats had undergone a complete destruction of the septum including medial and lateral septal nuclei with no spreading to more ventrally located structures (group 7 SI).

Of the 21 rats septalectomized at 3 months of age 19 had undergone a complete destruction of the septum that did not involve more ventrally located structures. These rats had been raised in groups from weaning (group 3d SG). The lesions were comparable to those performed at 7 days of age in both group-reared and isolation reared rats. A group of control rats had been sham operated at 7 days of age 22 rats being raised in groups from weaning (group 7 CG) and 31 rats being maintained in isolation from weaning (group 7 CI).

Open Field

In 40-day-old rats For this group the analysis of variance showed no lesion effect on locomotor activity over the three days but an environment effect and a lesion X environment interaction [$F(1,81) = 6.93$ $P < 0.05$ on the second day $F(1,81) = 17.06$ $P < 0.01$ on the third day] (Fig. 2). Individual group comparisons made with a Scheffé test revealed that early septal rats maintained in groups from weaning (7 SG) were more active than early septal rats maintained in isolation (7 SI) on the first day ($P < 0.05$). In contrast on the second day and on the third day the rats maintained in groups (7 SG) were less active than rats maintained in isolation (7 SI) ($P < 0.05$ and $P < 0.01$ respectively). This was due to the fact that ambulation activity of the 7 SG rats decreased drastically over the three days while activity of the 7 SI rats did not change from the first to the third day of the open field test.

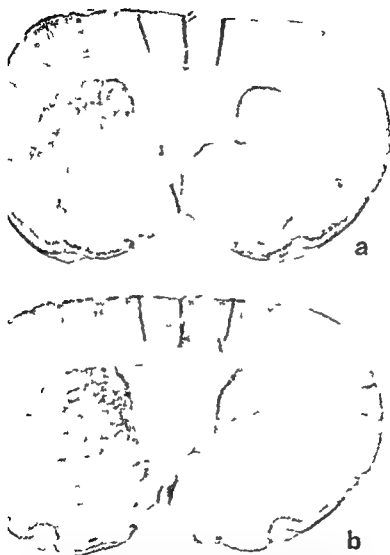


Figure 1. Photomicrographs of frontal sections through the septum from (a) a rat that had a lesion restricted to the septum at 7 days of age and (b) a rat that had a septal lesion invading more ventrally located structures at 7 days of age.

the third day [$F(1, 78) = 5.80$, $P < 0.05$]. Individual group comparisons made with a Scheffé test revealed that rats that had sustained septal lesions in infancy and had been maintained in groups from weaning (7 SG) were less active at adult age than sham-operated controls maintained in the same environment (7 CG) on the first day ($P < 0.01$) and also than rats 7 SvG on the first day ($P < 0.05$). These septal rats lesioned in infancy (7 SG) were also significantly less active than rats lesioned in adulthood (Ad SG) on the second day ($P < 0.05$) and on the third day ($P < 0.05$). However, when the rats septalectomized at 7 days of age had been maintained in isolation from weaning (7 SI), they were significantly more active at adult age than sham-operated controls maintained in the same environment (7 CI) on the second day ($P < 0.01$) and on the third day ($P < 0.01$). When septalectomized in infancy, rats maintained in isolation (7 SI) were reliably more active than rats maintained in groups (7 SG) on the second day ($P < 0.01$) and on the third day ($P < 0.05$). In the control groups, on the other hand, the group-reared rats (7 CG) were reliably more active than the isolation-reared rats (7 CI) on the first day of the open field test ($P < 0.05$).

Analysis of variance on the rearings made by the rats when adult revealed a significant lesion effect on the first day and on the third day [$F(2, 78) = 4.41$, $P < 0.05$] but no age effect and no environment effect. Individual group comparisons made with a Scheffé test revealed that on the first day the rats septalectomized in infancy and maintained in groups made significantly fewer rearings than the control rats maintained in groups on the first day ($P < 0.05$) and on the third day ($P < 0.01$) if the lesion was restricted to the septum. Scheffé test also revealed that rats septalectomized in adulthood (Ad SG) made reliably fewer rearings on the third day than sham-operated control rats ($P < 0.01$).

Analysis of variance on the number of boluses dropped in the open field revealed a lesion \times environment interaction on the first day [$F(1, 81) = 4.19$, $P < 0.05$] and an environment effect on the third day [$F(1, 81) = 6.44$, $P < 0.05$]. Individual group comparisons made with a Scheffé test revealed that on the first day the defecation scores were reliably higher in rats septalectomized (lesion restricted to the septum) at 7 days of age and maintained in groups (7 SG) than in control animals that had been sham-operated at the same age and maintained in groups from weaning (7 CG) ($P < 0.01$) and that they were also reliably higher than in rats septalectomized at adult age (Ad SG) ($P < 0.05$) and higher than in rats operated in the same area at 7 days of age and maintained in isolation from weaning (7 SI) ($P < 0.05$). On the third day the rats 7 SI defecated significantly more than the rats 7 SG ($P < 0.05$).

In short, septal lesions performed in 7-day old rats resulted at adult age (as has been observed at 40 days of age) in a reduced number of rearings in the open field. The decrease in the number of rearings did not depend on environmental conditions nor did it depend on the age (7 days or 3 months) at which the lesion had been performed. Ambulation activity displayed at adult age in the open field

lesioned rats depended on the age at which the septal lesion had been performed (rats lesioned at adult age did not show lower ambulation scores than did controls if one considers the activity summed over the three days of the test) and on the environmental conditions in which the animals had been reared from weaning (early septal group reared rats were less active than group reared controls while early septal isolation reared rats were more active than isolation reared controls). Concerning the defecation rate only rats septalectomized at 7 days of age and maintained in groups had a high defecation rate on the first day of the open field test performed at adult age.

A few major facts emerge from the data concerning the open field tests performed at 40 days of age and at adult age. In the first place it is worth noting that ambulation activity significantly decreased from the first to the third day in rats sham operated at 7 days of age (7 CG and 7 CI) as well as in rats septalectomized at 7 days of age and maintained in groups (7 SG and 7 SvG) but this activity did not vary from the first to the third day in rats septalectomized at 7 days of age and maintained in isolation (7 SI) nor in rats septalectomized at adult age (Ad SG).

Furthermore there occurred a marked decrease between 40 days and 3 months of age in the ambulation activity on the first day of the test in control rats group-reared (7 CG) or isolation reared (7 CI) and also in rats 7 SG. In contrast there was no significant difference between the activity measured on the first day at 40 days of age and that measured on the first day at 3 months of age in rats 7 SI and 7 SvG.

Concerning the number of rearings on the first day of the test the analysis revealed no reliable difference between 40 days and 3 months of age in the control rats (7 CG and 7 CI) while a marked decrease was observed in rats septalectomized at an early age (7 SG and 7 SI).

The defecation scores on the first day of the test decreased from 40 days to 3 months of age in septal rats 7 SG and 7 SI while they remained at the same level in control rats 7 CG and 7 CI.

Actigraphy

The data on actography were submitted to an analysis of variance using lesion, age of operation and environment as the main factors (Fig. 5). Total activity (summed over 24 hours) was compared for all animals with results showing a significant lesion effect [$F(1, 70) = 18.2$, $P < 0.01$]. Scheffé tests revealed that total activity of rats septalectomized at 7 days of age (7 SG and 7 SvG) or at adult age (Ad SG) was significantly higher than total activity of control rats sham operated (7 CG) at the same age ($P < 0.01$). When maintained in isolation the septal rats (7 SI) had a higher total activity than control rats (7 CI) ($P < 0.01$).

A further analysis of activity scores per hour revealed that immediately after introduction of the rats into the activity cage (between 11:30 AM and noon) there

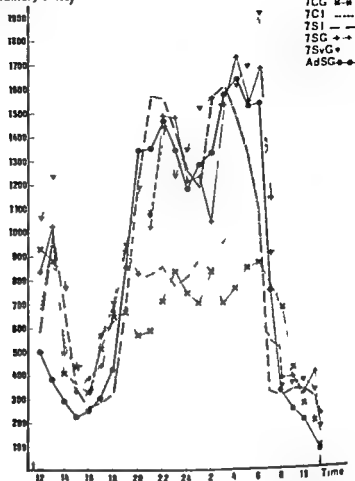
Mean Spontaneous Activity
(arbitrary units)

Fig. 5. Mean spontaneous activity measured for 24 consecutive hours beginning at 11:30 AM. For symbols of experimental groups see Figure 2. For significant differences, see Results section.

was no lesion effect but a reliable age effect and a reliable environment effect. Scheffé tests revealed that rats septalectomized at adult age (Ad SG) were significantly less active than rats septalectomized at 7 days of age (7 SG) ($P < 0.01$) and significantly less active than control rats ($P < 0.01$). Furthermore, control rats maintained in groups (7 CG) were more active than controls maintained in isolation (7 CI) ($P < 0.05$). Septal rats maintained in groups (7 SG) were more active than septal rats maintained in isolation (7 SI) ($P < 0.05$).

On and after 8 00 PM and until 6 00 AM rats septalectomized at an early age were more active than control rats sham operated at the same age irrespective of whether they had been group reared ($P < 0.05$) or isolation reared ($P < 0.05$). Rats septalectomized in adulthood were also more active than control rats during the period of time ($P < 0.05$).

The Scheffé tests revealed no significant difference between groups from 6 00 AM until 11 00 AM and this is precisely the period of the day during which the open field tests were performed. So differences observed with regard to the animals' behavior can hardly be due to differences in their spontaneous activity.

Mouse Killing Behavior

Of the 18 rats septalectomized at 7 days of age (lesion restricted to the septum) and group reared from weaning (7 SG) 10 (56%) displayed mouse killing behavior. Four animals killed the mouse within the first five minutes while six others killed during the night (four of the latter rats stopped killing after about one month). Eight rats never killed the mouse introduced in the home cage. Only one of the 11 sham operated rats maintained in groups (7 CG) proved to be a killer rat (9%). The 7 SG rats thus showed a significantly higher percentage (χ^2 with Yates's correction = 4.44) of muricidal responses than did the control animals (7 CG).

Of the 25 rats septalectomized at an early age (with a lesion extending to ventral structures) and maintained in groups (7 SvG) nine (36%) displayed mouse killing behavior. Six rats killed the mouse within five minutes following the introduction of the mouse while three others killed during the night. The comparison of the proportion of killer rats in group 7 SvG and group 7 SC positively did not reveal any significant difference ($\chi^2 = 1.62$). Like the 7 SG rats the 7 SvG rats exhibited a significantly greater percentage of muricidal behavior (χ^2 with Yates's correction = 8.93) than did the control rats maintained in groups (7 CG).

Of the 25 rats septalectomized at 7 days of age and maintained in isolation (7 SI) 13 rats (52%) killed the mouse introduced in their cage mostly during the night. The comparison of this percentage with the percentage of killers in the 7 SG rats revealed no significant difference ($\chi^2 = 0.05$).

Ten of the 31 (32%) sham operated rats maintained in isolation (7 CI) displayed muricide behavior either within five minutes following the introduction of the mouse into the rat's cage or during the night. They showed a relatively higher percentage (χ^2 with Yates's correction = 5.85) of muricidal responses than did the control rats maintained in groups (7 CG). While the percentage of killers in the septalectomized and maintained in isolation (7 SI) was higher than the percentage of killers in isolation reared control rats (7 CI) the χ^2 test revealed no reliable difference ($\chi^2 = 4.24$).

In the group of rats septalectomized at adult age ten of 17 animals (59%) displayed mouse killing behavior most of them killing the mouse during the night the others killing almost immediately. This percentage does not significantly differ from the percentage of killer rats in the 7 SG group ($\chi^2 = 0.04$).

Body Weight and Weight of Adrenals and Testes

Analysis of variance computed on body weight (Fig. 6) over 15 weeks (postnatal weeks 5–19) revealed a reliable lesion effect until the tenth week of age. Scheffé tests revealed that the body weight of animals septalectomized at 7 days of age (lesion restricted to the septum or lesion also invading more ventrally located structures) and maintained in groups was reliably lower than the body weight of control rats sham operated at the same age and maintained in groups ($P < 0.05$). Scheffé tests also revealed that during the period following the septalectomy in the adult animal i.e. 15–17 weeks of age the Ad SG rats had a body weight significantly lower than that of control rats ($P < 0.01$).

Concerning the weight of the adrenals and testes (Table II) the analysis showed an age effect [$F(1, 67) = 4.51$, $P < 0.05$ for the adrenals, $F(1, 67) = 28.4$, $P < 0.01$ for the testes]. Scheffé tests revealed that rats septalectomized at adult age (Ad SG) had heavier adrenals and testes than did control rats ($P < 0.05$ and $P < 0.01$) as well as rats septalectomized at 7 days of age and maintained in groups (7 SG) ($P < 0.05$ and $P < 0.01$).

Food Intake

Analysis of variance on the data concerning daily food intake (Table II) measured at adult age revealed a lesion effect [$F(2, 69) = 6.91$, $P < 0.01$] and an environment effect [$F(1, 65) = 4.65$, $P < 0.05$]. Scheffé tests revealed that the food intake of rats septalectomized at 7 days of age and maintained in groups (7 SG) was reliably higher than food intake of control rats ($P < 0.01$) and food intake of rats 7 SG ($P < 0.01$). Food intake of rats septalectomized at adult age (Ad SG) was significantly higher than that of control rats (7 CG) ($P < 0.01$). Moreover rats septalectomized in infancy ate more per day when group-reared than when isolation reared ($P < 0.01$).

DISCUSSION

First of all it appears that septal lesions performed in infancy have a lasting effect upon juvenile and adult behavior. Lowered rearing scores in the open field were already observed at the age of 40 days when locomotor activity (summed over the three days of the test) and defecation scores seemed to be unaffected. As a matter of fact the early septal lesion had an effect on locomotor activity since it entailed a deficient habituation provided that the lesioned animals were raised in isolation from weaning until the age of 40 days.

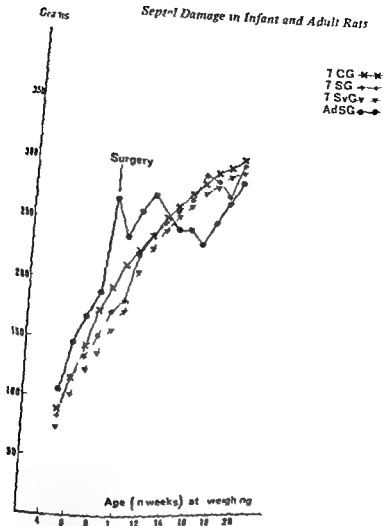


Fig. 6. Body weight in septal rats and control rats. For symbols of experimental groups see Figure 2. For significant differences see Results section.

When tested in the open field at adult age early septal rats group reared from weaning displayed less locomotor activity than did control rats or rats septalectomized at adult age. Once again, when raised in isolation from weaning, early septal rats showed a clearly deficient habituation in comparison with the group reared septal rats.

Sham operated rats reared in isolation (7 CI) were less active than group-reared control rats (7 CG) on the first day of the open field test. Just after being

TABLE II Food Intake and Weight of the Adrenals and of the Testes in Septal Rats and Control Rats (Mean \pm SE)

Rats	Food intake (gm) per day	Weight of adrenals (mg/100 gm body weight)	Weight of testes (mg/100 gm body weight)
7 CG	21.5 \pm 2.0	13.4 \pm 2.8	772.9 \pm 110.7
7 SG	23.7 \pm 2.5	13.1 \pm 3.7	753.7 \pm 89.5
7 SvG	21.5 \pm 1.7	12.3 \pm 2.7	759.7 \pm 87.3
Ad SG	24.7 \pm 2.3	15.3 \pm 2.7	942.5 \pm 108.6
7 CI	23.2 \pm 2.3	13.3 \pm 2.1	777.5 \pm 83.7
7 SI	21.2 \pm 2.1	13.7 \pm 1.8	779.5 \pm 107.6

introduced into the actography i.e. during the initial period that can be considered to correspond to the exploration of a novel environment. Isolation reared animals (whether septalectomized or sham operated) also proved less active than group reared animals. According to Sahakian et al [1977] isolated rats initiate exploratory sequences of behavior more often than controls but terminate them sooner.

In contrast with rats septalectomized in infancy and then group reared from weaning, those lesioned at adult age did not show lower ambulation scores than the group reared control rats. If one considers the locomotor activity summed over the three days of the open field test. As a matter of fact, this apparent absence of lesion induced change results from two effects that compensate each other, namely a lowered activity on the first day of the test and a deficient habituation on the following days.

A number of contradictory conclusions have been stated in the literature with regard to the effect of septal lesions on the rat's activity in various situations. Wallace et al [1978] found that damage restricted to the septum does not cause a reduction in horizontal activity, i.e. in the number of squares crossed. A decreased activity in the open field following septal lesions was reported by some authors [Corman et al 1967, Mos et al 1977, Schwartzbaum et al 1976]. A lesion induced decrease in activity was also found in activity cages [Gaze et al 1975], in running wheels [Clody et al 1969, Douglas et al 1976, Gotsick 1969, Nielson et al 1965] and in home cages [Thomas et al 1959, Zuckerman 1965]. In contrast, a lesion induced increase in activity was found in open field tests [Donovick et al 1969, Douglas et al 1966, Woodruff et al 1976], in mazes [Nielson et al 1965, Thomas et al 1959] and in other novel environments [Corman et al 1967, Gotsick 1969].

Such contradictions can be overcome only if one considers both the degree of familiarity with the test situation and the length of the period of time over which the activity is being summed. This statement may well be exemplified by

the behavior of our septal animals when submitted to 24 hour actography. During the initial exploration period rats lesioned in infancy were rather less active and those lesioned at adult age were clearly less active than sham operated control animals while they all showed clearly higher activity scores than controls later on i.e. during the night. One may thus assume that septal lesions result in increased activity levels when the situation is not too unfamiliar to the animal and/or when changes are introduced into familiar environments (we noticed that all septal rats tried to escape from their home cage every time the lid was raised) while a decreased activity is noted in unfamiliar situations and especially when the test is carried on for a short time only.

Whatever the age (7 days or 3 months) at which the rats had been septalectomized they exhibited lower rearing scores in the open field than did controls irrespective of the environmental conditions in which they had been reared from weaning. This decreased vertical activity (rearing) is in agreement with the findings of Beatty et al [1975], Darlam [1969], Kemble et al [1975] and Wallace et al [1978] following septal lesions carried out in the adult rat.

Defecation in the open field was differentially affected according to the age at which the septal damage occurred. Rats lesioned in infancy and reared in groups from weaning defecated more than controls on the first day of the open field test carried out at the age of 3 months while septal lesions performed in adulthood did not result in any reliable change in defecation rate. It is often assumed that activity and defecation in the open field reflect the rat's emotional reactivity. More specifically high activity and low defecation are thought to reflect low emotionality while low activity and high defecation are associated with high emotionality. When comparing the effects of septal damage in group-reared animals it appears that on the first day of the open field test a reduced ambulation activity was observed both after an early lesion and after a lesion performed at adult age (though less so in the latter case) while a significant increase in defecation was found only in early lesioned rats. On the other hand a deficient habituation over the three days of the test was observed in animals lesioned at adult age but not in group reared animals that had undergone the septal lesion in infancy.

It is worth adding however that irrespective of whether the lesioned induced syndrome (decreased ambulation on the first day, increased defecation on the first day, deficient habituation over the three days) was complete or not all septalectomized rats were clearly distinguishable from controls by the vigor and persistence of their escape response and their reaction to capture. When taken from their home cage and handled all septal rats reacted quite vigorously using their hind legs to push away the experimenter's hand but after being patted for a short while they became docile (more so than controls), submissive and placid. On the following day however the septal rats were again quite reactive to any attempt to catch them.

TABLE II Food Intake and Weight of the Adrenals and of the Testes in Septal Rats and Control Rats (Mean \pm SE)

Rats	Food intake (gm) per day	Weight of adrenals (mg/100 gm body weight)	Weight of testes (mg/100 gm body weight)
7 CG	21.5 \pm 2.0	13.4 \pm 2.8	77.9 \pm 11.1
7 SG	23.7 \pm 2.5	13.1 \pm 3.7	75.3 \pm 8.5
7 SvG	21.5 \pm 1.7	12.3 \pm 2.7	75.9 \pm 8.3
Ad SG	24.7 \pm 2.3	15.3 \pm 2.7	94.5 \pm 10.6
7 CI	23.2 \pm 2.3	13.3 \pm 2.1	72.5 \pm 8.7
7 SI	21.2 \pm 2.1	13.7 \pm 1.8	77.9 \pm 10.6

introduced into the actography is during the initial period that can be considered to correspond to the exploration of a novel environment. Isolation reared animals (whether septalectomized or sham-operated) also proved less active than group reared animals. According to Sahakian et al [1977] isolated rats initiate exploratory sequences of behavior more often than controls but terminate them sooner.

In contrast with rats septalectomized in infancy and then group reared from weaning, those lesioned at adult age did not show lower ambulation scores than the group reared control rats. If one considers the locomotor activity summed over the three days of the open field test. As a matter of fact, this apparent absence of lesion induced change results from two effects that compensate each other, namely a lowered activity on the first day of the test and a deficient habituation on the following days.

A number of contradictory conclusions have been stated in the literature with regard to the effect of septal lesions on the rat's activity in various situations. Wallace et al [1978] found that damage restricted to the septum does not cause a reduction in horizontal activity. In the number of squares crossed and increased activity in the open field following septal lesions was reported by some authors [Corman et al 1967; Mos et al 1977; Schwartzbaum et al 1966]. A lesion induced decrease in activity was also found in activity cages [Gale et al 1975], in running wheels [Clody et al 1969; Douglas et al 1966; Gotsick 1969; Nielson et al 1965] and in home cages [Thomas et al 1959; Zuckerman 1965]. In contrast, a lesion induced increase in activity was found in open field tests [Donovick et al 1969; Douglas et al 1966; Woodruff et al 1976], in mazes [Nielson et al 1965; Thomas et al 1959] and in other novel environments [Corman et al 1967; Gotsick 1969].

Such contradictions can be overcome only if one considers both the degree of familiarity with the test situation and the length of the period of time over which the activity is being summed. This statement may well be exemplified by

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Whatever the age (7 days or 3 months) at which the rats had been septalctomized they exhibited lower rearing scores in the open field than did controls irrespective of the environmental conditions in which they had been reared from weaning. This decreased vertical activity (rearing) is in agreement with the findings of Beatty et al [1975], Dirlam [1969], Kemble et al [1975] and Wallace et al [1978] following septal lesions carried out in the adult rat.

Defecation in the open field was differentially affected according to the age at which the septal damage occurred. Rats lesioned in infancy and reared in groups from weaning defecated more than controls on the first day of the open field test carried out at the age of 3 months while septal lesions performed in adulthood did not result in any reliable change in defecation rate. It is often assumed that activity and defecation in the open field reflect the rat's emotional reactivity. More specifically, high activity and low defecation are thought to reflect low emotionality while low activity and high defecation are associated with high emotionality. When comparing the effects of septal damage in group reared animals it appears that on the first day of the open field test a reduced ambulation activity was observed both after an early lesion and after a lesion performed at adult age (though less so in the latter case) while a significant increase in defecation was found only in early lesioned rats. On the other hand a deficient habituation over the three days of the test was observed in animals lesioned at adult age but not in group reared animals that had undergone the septal lesion in infancy.

It is worth adding however that irrespective of whether the lesioned induced "syndrome" (decreased ambulation on the first day, increased defecation on the first day, deficient habituation over the three days) was complete or not, all septalctomized rats were clearly distinguishable from controls by the persistence of their escape response and their reaction to capture. When taken from their home cage and handled, all septal rats reacted quite vigorously with their hind legs to push away the experimenter's hand but after being put back in a short while they became docile (more so than controls), submissive and placid. On the following day however the septal rats were again quite reactive to any attempt to catch them.

The lasting hyperemotionality that resulted from early septal damage contrasts with the rather transient character of the hyperemotionality that was often reported following septal damage in the adult rat [Ahmad et al 1968 Brady et al 1953 Corman et al 1967 Fried 1975 Gotsick et al 1972 Hammond et al 1971 Singh 1969 Slotnick et al 1973]. The effects resulting from early septal damage seem to depend on both the sex of the lesioned animals and the age at which the lesion was carried out. Endroczi et al [1969] found no change in emotionality in rats septalectomized on the third postnatal day when compared with controls at 2 months of age. Stewart et al [1977] reported that the emotionality scores were highest immediately after a septal lesion performed at the age of 25 days and that they fell to near control levels by 40 days of age. On the other hand, Phillips et al [1973] observed increased emotionality in female rats but not in males following septal lesions performed at 25 days. According to Phillips et al [1972] septal lesions produce a very transient (up to three days) hyperemotionality when carried out in prepubertal male rats (30–40 days of age) whereas similar lesions result in sustained hyperemotionality (up to 21 days) when carried out in postpubertal animals (45–55 days of age).

Our finding that the behavioral effects of early septal lesions limited to the septum are similar to those of lesions invading more ventrally located structures fails to replicate the findings of Turner [1970] and of Thomas et al [1971] following septal lesions performed at adult age. These authors presented strong evidence that lesions of the septum alone were not sufficient to produce an increased irritability and that lesions located in and below the horizontal plane of the anterior commissure were necessary for such an increased irritability to appear. On the other hand, Paxinos [1975] reported that destruction of the region ventral to the septum even though necessary was not sufficient for the appearance of an increased irritability and he suggested that it was some interaction effect of damage in both areas (septum and the ventral region) that actually produced such an effect.

Concerning body weight, the septal lesions had disruptive effects on weight gain whether they were performed at adult age or in infancy. The latter finding contradicts the results of Johnson [1972] but corroborates those of Molino [1975] who found disruptive effects on body weight after septal lesions performed at 10 days of age. The transient deficit in weight gain was not due to hypophagia since the control of food intake revealed that the rats lesioned in infancy as well as those lesioned at adult age actually ate more than control rats. There is an apparent contradiction between a reduced body weight and an increased food intake. It must be recalled however that the septal rats displayed a markedly enhanced spontaneous activity during the night. Our results are con-

consistent with those of Stoller [1972] who found an increase in food consumption in septal rats while their body weight was below the body weight of controls. Concerning the weight of adrenals and testes it appears that rats septalectomized at adult age have heavier adrenals and testes than control rats and rats castrated in infancy. Although some dichotomy may exist between the size of the adrenals and their functional capacity [Mangili et al 1966] changes in adrenal weight are useful in assessing the response of rodents to stress [Christian et al 1964]. Increased adrenal functions following septal damage were found by Endouzi et al [1960] in the cat and by Bohus [1961] in the rat. Usher et al [1967] found an increase in adrenal weight in rats stressed following septal lesions. Montgomery [1968] obtained adrenal enlargement in septal rats in response to excessive handling or to provocations during behavioral testing. Whatever the origin of such an enlargement of the adrenals (direct interference with the functioning of the pituitary-adrenal axis or increased activation of pituitary-adrenal functions relating to the increased emotionality or both) normal weight of the adrenals is recovered by the animals that have undergone septal lesion in infancy. The same holds true with regard to testicular weight since septal lesions performed at adult age affected the weight of the testes as was also found by Kling [1964] while early septal lesions did not.

As regards mouse killing behavior all septal lesions clearly increased the probability of its occurrence in the adult rat irrespective of whether the lesions were performed in infancy (at 7 days) or in adulthood (at 3 months) and irrespective of whether the animals were group reared or isolation reared from weaning. The increased probability of muricidal responses following septal damage performed in adulthood corroborates the findings of Siegel et al [1969], Miczek et al [1972] and Latham et al [1974]. It is worth adding that in rats castrated in infancy the mouse killing behavior proved to be rather unstable as was reported with regard to septal damage performed at adult age. Some rats stopped killing mice for some time and then started killing again.

The discrepancies that exist in the findings relative to the effect of septal damage on interspecific aggressiveness depend on a number of factors. Whether a rat will kill a mouse on the first postoperative test depends in part on the time of postoperative testing since less killing occurs at longer postoperative delays. The longer delay used for testing septal rats could at least partially explain the low percentage of killer rats obtained by Miky et al [1972]. Indeed, Miczek et al [1972] found that on the first postoperative day the septal rats displayed increased fighting in response to shock and that muricide was equivalent. About ten days following surgery both these effects began to disappear and they were no longer found by postoperative day 15. Such a parallel

evolution suggests that increased reactivity and increased probability of attack are causally related contrary to the conclusions of Ahmad et al [1968]

2 Extensive exposure to mice prior to septal surgery may entail a stable inhibition of the mouse killing behavior so that killing following the lesion does not occur [Miley et al 1972 Penot et al 1976] This explains why no muricide was observed in septal rats that had been given prolonged experience with mice prior to the operation [Karli 1960]

3 The length of the muricidal test may also account for some discrepant results The test employed by Malick [1970] was short (five minutes) and this may explain the lack of increase in muricide that he observed following septal damage Most experimenters have used longer tests and Raper et al [1977] have emphasized the importance of the test length

4 Site and extent of the septal lesion may also affects its outcome with regard to muricide But contrary to the report of Wallace et al [1978] who found that septal damage performed in the adult rat results in increased muricide if it extends to more ventrally located structures we found in the present study that early septal damage had the same outcome with regard to mouse killing behavior whether the lesion was restricted to the septum or invaded ventral structures in addition

As recalled above familiarization with mice results in a rather stable inhibition of mouse killing behavior Since septal lesions do not abolish this kind of behavior while corticomedial amygdaloid lesions do have such an effect [Eclancher et al 1975 Karli et al 1977] one can conclude that the septum is not an essential link in the chain of mechanisms through which social interactions with mice result in a stable inhibition of muricide But inhibition of muricide can also result from interactions with conspecifics This was observed previously in rats that had undergone a removal of the olfactory bulbs [Karli et al 1974] In the present study the incidence of muricide in group reared controls was reliably lower than in isolation reared controls The fact that this difference was no longer observed in septal rats suggests that the septum is somehow involved in the mechanisms through which interactions with conspecifics result in a suppression of muricide (by an overall negative reinforcement of aggression?) In other words even if a brain lesion provokes an increased probability of occurrence of muricide behavior one has to take account not only of a possible increase in general reactivity and/or emotionality but also of a possible interference with the development and/or maintenance of a more or less stable inhibition of muricide resulting from interactions with mice or with conspecifics

In many respects the behavior of rats septalectomized at 7 days of age was closer to that of rats septalectomized at adult age than to that of sham operated control rats In other words there occurred no total sparing of function following an early septal damage The sparing of function that actually occurred may be due to the environmental conditions in which the lesioned animals were reared

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Maternal Aggression in Mice. The Non-Specific Nature of the Exteroceptive Maintenance by Young

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Five hours of pup removal during early lactation (Postpartum Day 6) reduced maternal aggression in mice while placement of the dam's entire litter (six pups) or a single pup behind a double wire mesh partition in the homecage maintained aggression at a level identical to that of mothers in direct contact with their young. When placed behind the partition unfamiliar 6, 13 and 20-day-old pups but not 30-day-old mice maintained the behavior as effectively as the dam's own young. The relationship of the findings to communal rearing conditions in the mouse is discussed.

Keywords: mice, maternal aggression, young, exteroceptive stimuli

INTRODUCTION

Maternal aggressive behavior has been observed in many mammalian species, both in both confined and free ranging conditions (cf. Rheingold, 1963; Hafez, 1969). Recent controlled laboratory studies in mice have begun to unravel the mechanism(s) controlling the behavior (Svare, 1977). Several lines of evidence indicate that nipple growth and the presence of olfactory stimulation from young are prerequisites for the initiation of maternal aggression. First, females that are thelectomized (nipples removed) prior to

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parturition and that are continuously fostered young following delivery and males whose young are removed following parturition each fail to exhibit fighting behavior [Gandelman and Svare 1974 Svare and Gandelman 1976a] Second virgin females which lack the nipple growth that normally occurs during pregnancy fail to show maternal aggression following repeated exposure to young [Svare and Gandelman 1976b] Third virgin females can be induced to exhibit maternal aggression by treatment with a hormone regimen that induces nipple growth (19 daily injections of 500 μ g progesterone and 0.02 μ g estrogen) followed by suckling stimulation from foster young [Svare and Gandelman 1976b] Fourth hormone primed virgin females like pregnant and normal parturient males are nonaggressive prior to suckling exposure and fail to exhibit aggression following either the removal of young or following thelectomy combined with the presentation of foster young [Svare and Gandelman 1976b] Fifth hysterectomy and the fostering of young on or before Day 12 of gestation (the normal gestation period of the mouse is 18 days) a time at which nipple growth is not maximal and pup attachment does not take place does not result in fighting behavior [Gandelman and Svare 1974 Svare Bartke and Guislin 1978] Finally hysterectomy and the fostering of young after Day 13 of gestation a time at which nipple growth is adequate for pup attachment results in normal numbers of animals fighting [Gandelman and Svare 1974 Svare et al 1978]

While suckling is clearly involved in the initiation of aggression and perhaps the declining intensity of fighting with advancing lactation [Svare 1977] it may not be needed for the short term maintenance of fighting behavior. This is suggested by our findings showing that removal of young for 5 hours from the home cage during early lactation (Postpartum Day 6) eliminates aggression whereas placement of young behind a wire mesh partition in the dam's home cage for the same period of time maintains the behavior [Svare and Gandelman 1973] Qualitative and quantitative assessments of maternal aggressive behavior were lacking in the above study (only the presence or absence of fighting was observed) thus leaving in doubt whether exteroceptive stimuli from young are really as effective in maintaining aggressive behavior as direct contact with pups. In addition a number of other questions remain to be answered concerning the specificity of the pup-related stimulus involved in the exteroceptive maintenance of aggression.

In the first experiment we sought to answer the following questions: a) Is the maternal aggressive behavior exhibited by lactating females maintained in the presence of nonphysical contact with young qualitatively and quantitatively similar to that of animals in direct contact with their young? b) Are unfamiliar young as effective as the mother's own young in maintaining the behavior in the absence of direct physical contact? c) Is one pup as effective as the dam's entire litter in the exteroceptive maintenance of the behavior?

EXPERIMENT 1

Method

Pregnant primiparous Rockland-Swiss (R-S) albino mice 70-80 days of age were housed individually in 11 X 7 X 5 translucent cages the floors of which were covered with wood shavings. The mice had free access to food (Purina Laboratory Chow) and water and were maintained on a 12/12 hr light/dark cycle with lights on between 7 am and 7 pm. Behavioral testing began at 3 pm.

Screening of animals for maternal aggression was necessary because 20% of lactating R-S mice do not exhibit the behavior. Thus, on Postpartum Day 5 (litters had been adjusted to six pups on the day of parturition) an adult male R-S mouse that had been group housed with five other cage mates was introduced into the homecage of each dam 3 min after the removal of its young. The young were removed to prevent them from being trampled upon during the fighting test. This period of pup removal which was also used on subsequent tests has been shown not to influence maternal aggression [Gandelman 1972a]. The lactating animal was scored as exhibiting aggression if it attacked (ie bit and chased) the intruder during the 3 min test. The intruder animal was removed as soon as an attack was observed. Intruder animals rarely if ever attack lactating animals nor do they fight back in response to being attacked [cf Svare 1977].

At 9 am on Postpartum Day 6 75 lactating animals that had exhibited maternal aggression during the screening tests were randomly divided into 5 groups of 15 animals. (The Postpartum Day 6 was selected for study because by this time R-S mice exhibit peak levels of maternal aggression and because the exteroceptive maintenance of the behavior by young is fully functional [Svare and Gandelman 1973 Svare 1977]). The aggressive behavior of the lactating females was assessed following 5 hours of either pup removal (Group Removed) direct contact with their own young (Group Own-contact) placement of all of their own pups behind a double wire mesh partition extending 3 inches from the short wall of the homecage (Group Own partition) removal of all but one pup which was placed behind the partition (Group 1 - own partition) or removal of the mother's own young followed by the placement of a litter of similar age unfamiliar pups behind the partition (Group Unfamiliar partition). Three minute aggression tests were conducted in the homecages as previously described with the exception that the fighting was allowed to continue and the number of attacks were recorded.

Results

As seen in Table 1 5 hours of pup removal dramatically reduced maternal aggression while non physical contact with young for the same period regardless of

TABLE I Aggressive Behavior of Lactating Rockland Swiss Albino Mice Maintained in the Presence of Nonphysical Contact With Their Own or Unfamiliar Young of Different Ages

Experiment	Group	Proportion and % fighting	Median (and range) attacks
1 ^b	Removed	5/15 (33) ^a	7.0 (3-17)
	Own-contact	15/15 (100)	20.0 (8-47)
	Own-partition	15/15 (100)	16.0 (3-78)
	1-own-partition	14/15 (93)	15.0 (2-31)
	Unfamiliar-partition	14/15 (93)	15.5 (7-33)
2 ^c	6-partition	15/15 (100)	13.0 (5-31)
	13-partition	15/15 (100)	16.0 (2-27)
	20-partition	13/15 (87)	10.0 (7-74)
	30-partition	4/15 (27) ^a	11.0 (5-77)

^aSignificantly different from all groups ($P < 0.01$)

^bThe aggressive behavior of lactating females towards an adult male following 5 hr of either pup removal (Group Removed) direct contact with their own young (Group Own-contact) replacement of all of their own pups behind a wire mesh partition in the homecage (Group Own-partition) removal of all but one pup which was placed behind the partition (Group 1-own-partition) or removal of the mother's own young followed by the immediate placement of a similar aged litter of unfamiliar pups behind the partition (Group Strange-partition)

^cLactating animals had their own young removed and then were proffered either a single 6, 13, 20, or 30-day-old mouse behind a double wire mesh partition in the homecage. Testing for aggressive behavior toward an adult male was conducted 5 hr later.

the quality (own or unfamiliar) or quantity (1 or 6 pups) of the pup related stimuli maintained maternal aggressive behavior in a manner identical to that of lactating animals in direct contact with their young. Chi square tests revealed significant group differences in the proportion of animals fighting ($\chi^2(4) = 44.7$, $P < 0.001$). Significantly fewer animals fought in Group Removed than in any other group ($\chi^2(1) \geq 9.19$, $P < 0.01$). Moreover, a Kruskal Wallis One Way Analysis of Variance Test showed that the intensity of fighting behavior was not different influenced by the treatment conditions ($H(4) = 4.79$, $P > 0.05$). A Mann-Whitney U Test showed that the intensity of fighting behavior displayed by the small number of animals fighting in Group Removed was significantly lower than that of Group Own-contact ($U = 9.5$, $P < 0.05$).

Our observations of maternal aggression revealed that the animals of the different groups were qualitatively similar in their behavior. Attacks were initiated

(mean less than 3 sec) with biting directed toward the flanks and neck of the intruder. Ano genital sniffing and tail rattling frequently were seen between litters but never as a prelude to the initial attack. Intruder animals never initiated an attack against the lactating animals and never responded to attack by fighting back.

The above findings suggest that the stimulus from young responsible for the exteroceptive maintenance of aggression may be nonspecific in that unfamiliar pups are as effective as the mother's own young in maintaining the behavior. In the next experiment we further examined the specificity of the exteroceptive-related stimuli by analyzing the aggressive behavior of lactating animals maintained in non physical contact with unfamiliar pups of different ages. Because aggressive behavior begins to wane by Postpartum Day 8 and is virtually absent by Postpartum Day 15 [cf Gandelman 1972a; Svare and Gandelman 1973; St. John and Corning 1973] we predicted that the ability of pups to exteroceptively maintain maternal aggression would diminish with advancing

EXPERIMENT 2

Method

Sixty lactating female mice that exhibited maternal aggression during the nesting tests as previously described were randomly divided into 4 groups of 15 animals each. On Postpartum Day 6 the animals' own young were first removed and in their place we proffered either a single (Group 6-partition) 13-day-old pup (Group 13-partition) 20-day-old pup (Group 20-partition) or 30-day-old mouse behind a double wire mesh partition in the homecage. Aggression tests were conducted 5 hours later according to the procedure outlined in Experiment 1.

Results

The results showed that nonphysical contact with a single 6-, 13- or 20-day-old pup for 5 hours maintained maternal aggressive behavior at near normal levels comparable with Groups Own-contact and Own-partition of Experiment 1) while exposure to a 30-day-old animal did not maintain the behavior (compare Group Removed of Experiment 1) (see Table I). Chi-square tests showed significant group differences in the number of animals exhibiting aggression ($\chi^2(3) = 15.5$, $P < 0.001$). Significantly fewer animals exhibited aggression in Group 30-partition than in any other group ($\chi^2(1) = 8.69$, $P < 0.01$). Differences among the pups in the number of attacks were not statistically significant (Kruskal Wallis ANOVA Test $H(3) = 3.45$, $P > 0.05$). The above findings further suggest that the stimulus from young responsible for the exteroceptive maintenance of aggression

may be relatively nonspecific in that unfamiliar pups ranging from 6–70 days of age are also effective in maintaining the behavior.

DISCUSSION

The present study confirms our previous findings [Svare and Gandelman 1973; Svare 1977] by demonstrating that direct physical contact with young is not a prerequisite for the short term maintenance of maternal aggression in lactating mice. The removal of young for 5 hours from the homecage during early lactation (Postpartum Day 6) eliminates aggression while the placement of young behind a wire mesh partition in the dam's homecage maintains the behavior (Experiment 1). The current data extend the initial reports by showing that the quality (topography) and quantity (number of attacks) of aggression exhibited by lactating animals maintained in nonphysical contact with young is identical to that of dams left in direct contact with their pups.

Our findings also show that the pup related stimulus responsible for the exteroceptive maintenance of aggression is relatively nonspecific. When placed behind a wire mesh partition in the homecage, unfamiliar young between 6 and 70 days of age but not 30 days of age maintain aggressive behavior during early lactation as effectively as the dam's own young (Experiments 1 and 2). Moreover, one pup is as effective as the dam's entire litter in maintaining the behavior (Experiment 1). The function of these adaptations may be to ensure the protection and survival of unfamiliar young as well as pups that inevitably become separated from the nest and from their littermates as they grow older. The fact that wild and laboratory reared mice exhibit communal rearing of young [Crowcroft and Rowe 1961; Gandelman et al. 1970] would almost require the existence of such an adaptation. However, it is somewhat paradoxical that older pups possess the cues necessary for the exteroceptive maintenance of maternal aggression since it is well known that the behavior is absent after Postpartum Day 15 [Gandelman 1973a; Svare and Gandelman 1973; St. John and Corning 1973].

This striking lack of synchrony between the mother's changing behavior and the sensory cues provided by young is difficult to explain. It is well known that 6–20-day-old mice are defenseless and readily attacked by adults [Gandelman 1972b; Svare, Bartke, and Macrides 1978] while 30-day-old animals begin to become more independent and to take on the behavioral and physical characteristics of adults [cf. Williams and Scott 1953]. Thus, in a communal situation it would seem adaptive for at least some females (early lactating) to be responsive to the aggression maintaining cues of older but still defenseless pups. This interpretation requires us to invoke a theory of "division of labor" in the mouse social organization wherein one of the primary duties of the recently parturient female would be to defend young while that of late lactating animals would be to perform other important functions (i.e. foraging for food). Further studies of maternal

maternal aggression in communal situations clearly are necessary in order to support the above interpretations.

An issue not addressed in the present experiments concerns the mechanism responsible for the exteroceptive maintenance of aggression. Because smell plays a dominant role in modulating rodent social behavior and endocrine function [cf Doty 1976] we have speculated elsewhere that olfactory cues from young sustain maternal aggression by maintaining the release of circulating hormones in the dam [Svare 1977]. Regardless of the mechanism involved, the present findings indicate that the sensory cue from young is age-dependent (ie it is by 30 days of age) and is not specific to the mother's own young. Recent reports indicate that approach behaviors and home orientation by the young are controlled in part by exteroceptive stimuli (pheromones) emitted by mother [Porter et al 1976, Breen et al 1977]. The present findings as well as previous reports [Svare et al 1973, Svare 1977] indicate that the converse of this may also be true, namely, exteroceptive stimuli from young guide the protective behavior displayed by the mother.

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A Cross-Cultural Study of Rape

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Rape is often considered a crime and, as such, is subject to punishment. This paper reports a test of a "deterrence theory" of rape with a cross-cultural study which uses a sample of societies drawn from the Human Relations Area Files. A fraternal interest group theory is also tested. This theory argues that the presence of fraternal interest groups, power groups of related males, predicts the occurrence of rape in a society. Although the results support both theories, a composite theory using both deterrence and fraternal interest group theories was found to provide a better explanation for the occurrence of rape than either theory alone.

Rape, the act of having sexual intercourse with a woman forcibly and without her consent, is an ancient social problem which has concerned men and women in societies at all levels of social and political complexity. It is often considered a crime — indeed, most definitions state that it is a crime [Coughlin 1975: 295; Webster 1973: p. 1494] and, as a crime, it is frequently subject to punishment. Inherent in the belief system of some cultures, including those in Western civilization, is the notion that the application of punishment will prevent rape. This belief constitutes a "deterrence theory" of rape. This paper reports a cross-cultural study of rape in which this theory is tested using a sample of societies drawn from the Human Relations Area Files. A second theory, fraternal interest group theory, is also tested. Unlike deterrence theory, which sets forth a condition of punishment — for the suppression of rape, fraternal interest group theory sets forth the conditions which give rise to high frequencies of rape. The theory argues that the presence of fraternal interest groups, which are power groups of related males that resort to aggression to defend members' interests, predicts the occurrence of rape in a society.

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METHODOLOGY

Sample

The cross cultural survey or hologetic method is used to test the theories. Such a cross-cultural study typically utilizes a large sample of nonliterate societies often they are drawn from the Human Relations Area Files (HRAF) a massive compilation of indexed but uncoded ethnographic material on nearly 300 societies [Lagacé 1974]. While several steps are normally followed in conducting a cross-cultural study [Otterbein 1969] the essence of the method is the simultaneous examination usually by statistical methods of a set of variables common to the entire sample thus the hologetic method is a way of processing a large number of case studies at once. The sample used in this study was drawn from HRAF by Minturn Grosse and Haider to demonstrate the Cultural Pattern of Sexual Beliefs and Behavior [1969]. Included in the study were two variables dealing with rape. Codes for each variable were included. Data on other variables were taken from other sources, one source — the Ethnographic Atlas [Murdock 1962-1967] — contained coded data for most of the societies in the sample the other source [Otterbein and Otterbein 1965] for only a small number of these societies.

Measures

To test the above theories data were obtained on the frequency of rape its punishment the presence of fraternal interest groups and the frequency of feuding. Seven point scales were used by Minturn Grosse and Haider [1969 p 315] to obtain data on the frequency and punishment of rape.

Frequency of Rape for Men

- 1 Concept of rape is absent or rape reportedly never occurs
- 2 Rape does not occur but the concept is present
- 3 Rape is very rare
- 4 Some aggressive seduction is reported
- 5 Rape is not uncommon
- 6 Rape or aggressive seduction is the preferred form of sexual activity
- 7 All sexual relations are viewed as aggressive

Punishment of Men for Rape

- 1 Death
- 2 Exile
- 3 Heavy official fines or punishment by government
- 4 Fine paid to woman's family or small fine paid to government
- 5 Man may or may not be punished depending upon the sex partner
- 6 No official punishment or social stigma man is ridiculed
- 7 No punishment fine or social stigma

Code 4 data for the other variables derive from other sources. The procedures used in indexing fraternal interest groups are identical to those followed in previous studies [Otterbein and Otterbein 1965 p 1471 Otterbein 1968a p 278]

Two factors which should lead to the formation of fraternal interest groups are a marital residence pattern in which the new family lives with or near the groom's relatives and the presence of polygyny. Both indices were derived from the codings given by Murdock in the Ethnographic Atlas [1962 pp 117-118]. A society was considered to be *patrilocal* if the residence pattern was listed as patrilocal (P)* avunculocal (A) virilocal (V) ambilocal or where the majority of couples live with the groom's relative (D) or where a common household is not established but the men of the community either remain in their natal households or live in special men's houses (O). Societies were coded as *other* if the residence pattern was matrilineal (M) uxorilocal (U) neolocal (N) or ambilocal where the residence was not consistently with the kin of either spouse but was determined by personal circumstances (B C). The symbols in column 14 of the Atlas [1962 p 116] were used to code for the presence of polygyny (P Q R and S or E F and G with either p q r or s following) and its absence (H I J K L M N and O).

Code 5 data on residence and polygyny came from the Ethnographic Atlas [Murdock 1962 1967].

Codes for the frequency of feuding were taken from Otterbein and Otterbein [1965 p 1470].

Feuding was defined as blood revenge following a homicide. Ethnographic materials available in the Human Relations Area Files (HRAF) were used for this measure and were coded on a three point scale: frequent, infrequent or absent. A society was considered to have frequent feuding if after a homicide the kin of the deceased was expected to take revenge through killing the offender or any member of his kin group. If the kin of the deceased sometimes would accept compensation in lieu of such revenge the society was coded as having infrequent feuding. Feuding was considered to be absent in those societies which had formal judicial procedures for punishing the offender which always settled such matters through compensation or which were reported to rarely have homicide.

Code 6 data on rape were coded on a three point scale: frequent, infrequent or absent. This sample differs from the sample having data on rape: the number of societies found both in this sample and the rape sample is small.

Letters in parentheses are code symbols used in column 16 of the Ethnographic Atlas. The problem confronting any future cross-cultural study of rape is data paucity. In the case of 135 societies data were found on frequency for 43 societies and on punishment for 135 societies. It has been the awareness of data paucity brought to my attention first by F. Griffiths who has conducted a cross-cultural study of crime which has deterred me from drawing my own sample and training coders. During the spring of 1977 two students in my cross-cultural studies under my direction in HRAF encountered great difficulties in gathering data on rape for most societies.

RESULTS

Fraternal Interest Group Theory

Nearly twenty years ago van Velzen and van Wetering set forth fraternal interest group theory [1960] to explain why some societies were internally peaceful while others were non-peaceful. They argued that a fraternal interest group, which is a power group of related males, resorts to aggression when the interests of one of its members are threatened [1960 p 179]. The authors set forth their theory in the following manner [1960 p 180]

(1) In societies with power groups every act of violence elicits a chain reaction and there is danger of any individual deed of aggression leading to group conflict. Much intra-societal aggression can be attributed to the existence of power groups. Where they are not present there will be no struggle for power at group level.

(2) Violence can be more effectively suppressed if the individual concerned is not part of a power group which is ready to support him through thick and thin. Bystanders who separate and restrain combatants can curb a great deal of potential aggression. The individual lacks the psychological assurance of a reliable stronghold behind him.

(3) In societies where there are no power groups differences in power will merely consist of differences in muscular strength and personality. And violent treatment of the socially weak is also much less frequent.

Cross-cultural support was found for the hypotheses derived from the theory. The theory was elaborated and extended by Otterbein and Otterbein to encompass two forms of intergroup violence — feuding (which occurs between kinship groups within a political community) and internal war (which occurs between political communities within the same culture). In two cross-cultural studies it was shown that the presence of fraternal interest groups predicts feuding and internal war [Otterbein and Otterbein 1965; Otterbein 1968a, 1968b].

The presence of fraternal interest groups was indexed either by patrilocality or polygyny. Patrilocality, residence in which related males live close together, was argued to result in a settlement pattern in which related males live close together. When such a condition exists the men will look after each other's interests and welfare. Polygyny produces a similar situation: adult unmarried half brothers may be living near each other because polygyny frequently delays marital age for young males. The absence of fraternal interest groups was indexed by matrilocality or some other form of residence. If residence practices and marriage rules result in the scattering of related males over a large area, it is difficult for them to support each other's interests.

Fraternal interest group theory as noted above has been used to explain high incidences of interpersonal violence within local groups feuding and internal war. The theory can be expanded to encompass rape which is a form of interpersonal violence. Since it has been shown that societies with fraternal interest groups are internally non peaceful and that rape is a violent act it can be predicted that societies with fraternal interest groups will have high frequencies of rape. Indeed rape may be directly associated with other forms of violence. Societies with fraternal interest groups are societies which engage in feuding and internal war. It is often noted in the ethnographic literature that rape is a cause of feuding and warfare. On the other hand one aggressive act of fraternal interest groups may be to attack and rape women. It appears from ethnographic accounts that the motive is often to defile the enemy by violating his women valued possessions of the enemy. Thus feuding and internal war can be precipitated by rape or rape may be an aggressive act resulting from feuding or warfare.

Since rape is a violent sexual act of an individual male fraternal interest group theory as an explanation for rape can be questioned because the theory stresses both group action and group responsibility. Ethnographic accounts however indicate that rape is often perpetrated by several males for example the Hausa of northeastern Nigeria frequently become embroiled in internal wars due to raids which resulted in abduction or rape [Otterbein 1968c p 208]. Brownmiller's [1975] comprehensive review provides many examples of gang rape. Furthermore even if a man acts alone he has the support of male kin if he is a member of a fraternal interest group. Indeed it is his awareness of such available support which is a key element in fraternal interest group theory [van Velzen and van Veenning 1960 p 180].

From this theory the following hypothesis can be derived: *Societies with fraternal interest groups are more likely to have a high frequency of rape than societies without fraternal interest groups.* The hypothesis was tested by indexing with the presence or absence of patrilocal residence. The relationship between residence and frequency of rape is shown in Table I. The frequency of rape variable was dichotomized as close to the median as possible. 1-3 = low frequency, 4-7 = high frequency. A moderately strong correlation ($\phi = 0.36$) which is statistically significant ($0.01 < P < 0.02$) is obtained. The hypothesis can also be tested by indexing with the presence or absence of polygyny. The relationship between polygyny and frequency is shown in Table II. A weak non significant correlation ($\phi = 0.16$) is obtained. It can be cautiously concluded on the basis of these two tests that there is moderate support for the hypothesis.

Jacon Child and Barry [1963 p 294] found that polygynous households were associated with a high frequency of personal crime (by definition rape was considered a personal crime). This result is consistent with the hypothesis.

TABLE I Relationship Between Residence and Frequency of Rape

Residence	Frequency of rape		
	Low	High	Total
Patrilocal	9	16	25
Other	13	5	18
Total	22	21	43

$$\phi = 0.36 \quad \chi^2 = 5.50 \quad 0.01 < P < 0.02$$

TABLE II Relationship Between Polygyny and Frequency of Rape

Polygyny	Frequency of rape		
	Low	High	Total
Polygyny present	9	12	21
Polygyny absent	13	9	22
Total	22	21	43

$$\phi = 0.16 \quad \chi^2 = 1.13 \quad n.s. = \text{no significance}$$

A second hypothesis can be derived from the theory. Societies with a high frequency of rape are more likely to have frequent feuding than societies with a low frequency of rape. The relationship between feuding and frequency is shown in Table III. A strong correlation ($r_s = 0.75$) which is statistically significant ($P < 0.005$) is obtained. However, the small number of cases ($N = 14$) requires cautious acceptance of the results. (No test was made for the relationship between internal war and frequency because only five cases were available.) Since no relationship has been found for both hypotheses derived from fraternal interest group theory, it can be concluded that there is some support for the theory.

Deterrence Theory

The notion that certain behavior on the part of individuals or groups can be prevented by prior appropriate actions is known as deterrence theory. Scholars of military affairs have argued that an efficient military organization can be

TABLE III Relationship Between Frequency of Rape and Feuding

Frequency of rape	Frequency of feuding			
	Frequent	Infrequent	Absent	Total
Low	0	4	3	7
High	3	2	0	5
Total	3	6	3	12

$\chi^2 = 0.75$ $P < 0.005$ using Fisher's Exact Test *

* For the calculation of Fisher's Exact Test the trichotomized variables in this and each of the following tables were dichotomized as close to the median as possible

ould be aggressors from attacking [Otterbein 1970 p 88-92] while students of crime have argued that punishment or the threat of punishment will deter potential criminals from committing crimes [Kadish and Paulsen 1975 p 21-33 Packer 1968 p 39-48] Deterrence theory as applied to the study of criminal behavior has been delineated as follows [Packer 1968 p 39]

The classic theory of prevention is what is usually described as deterrence the inhibiting effect that punishment either actual or threatened will have on the actions of those who are otherwise disposed to commit crimes Deterrence in turn involves a complex of notions It is sometimes described as having two aspects after the fact inhibition of the person being punished special deterrence and inhibition in advance by threat or example general deterrence

Forcible rape is considered one of the four most serious crimes in the United States Along with willful homicide aggravated assault and armed robbery it is viewed as being appropriately subject to the criminal sanction [Packer 1968 296-301] A major purpose for applying a criminal sanction is to prevent or alter an act Deterrence theory is found in the literature on rape prevention Downmiller's study concludes with a series of recommended changes in sexual assault legislation which are intended to deter rape [1975 p 379-389] She states [1975 p 379]

I am one of those people who view a prison sentence as a just and lawful societal solution to the problem of criminal activity the best solution we have at this time as civilized retribution and as a deterrent against the commission of future crimes

From this deterrence theory of rape can be derived the following hypothesis *The greater the punishment for rape the less likely that rape will occur* In testing the hypothesis the seven point scale of punishment of men for rape was trichotomized 1 2 3 = major punishment 4 5 = minor punishment and 6 7 = no punishment Frequency of rape was measured as above with a dichotomous variable The relationship between punishment and frequency is shown in Table IV A strong negative correlation ($r_c = -0.68$) which is statistically significant ($P < 0.025$) is obtained This inverse relationship between the severity of punishment and the frequency of rape provides support for the hypothesis and the theory from which it is derived *

Further Analysis

Examination of the hypothesis test results indicates more support for deterrence theory than for fraternal interest group theory Although the correlations are not directly comparable — the ϕ coefficient is related to the Pearson r while r_c is not — the magnitude of the difference between a ϕ of 0.36 (see Table I) and a r_c of 0.68 ignoring the negative sign (see Table IV) suggests that the latter test result is the stronger Both the significance levels and visual inspection of the tables support this conclusion Rather than concluding that there is more support for deterrence theory than for fraternal interest group theory it is possible — using a three variable analysis — to examine the interaction between fraternal interest groups and punishment and their joint effect upon the frequency of rape in societies The procedure followed here is to reexamine the results of Table IV by

TABLE IV Relationship Between Punishment and Frequency of Rape

Punishment	Frequency of rape		Total
	Low	High	
Major	8	3	11
Minor	3	4	7
None	0	10	10
Total	11	17	18

$r_c = -0.68$ $P < 0.025$ using Fisher's Exact Test

*Controlling for level of political complexity using codes from the Ethnograph Atlas [Murdock 1967 : 160] has no measurable influence upon the relationship. The inverse relationship holds for both decentralized and centralized political communities.

controlling for the presence and absence of fraternal interest groups using the two measures of fraternal interest groups – patrilocality and polygyny (see Tables V and VI) Since the results of the three variable analysis using either index are nearly identical Tables V and VI will be discussed simultaneously

Three important findings emerge from the three variable analysis 1) Stronger results are obtained for deference theory if fraternal interest groups are absent than if they are present (compare the right side of Tables V and VI with the left side of the same tables) Both visual inspection and the larger τ_c s support this finding 2) The deviant cases in Table IV (ie cases in which major punishment is present and the frequency of rape is high) are explained by the presence of fraternal interest groups All three of these cases have both polygyny and patrilocal residence and are to be found on the left side of Tables V and VI Looked at in another way when fraternal interest groups are present major punishment and a high frequency of rape in a society are as likely to occur together as not (about a

TABLE V Relationships Among Punishment Frequency of Rape and Residence

Punishment	Patrilocal			Other		
	Frequency of rape			Frequency of rape		
	Low	High	Total	Low	High	Total
Major	3	3	6	5	0	5
Minor	1	3	4	2	1	3
None	0	6	6	0	4	4
Total	4	12	16	7	5	12

$$\tau_c = -0.42 \text{ not significant}$$

$$\tau_c = -0.81 \text{ } P < 0.05 \text{ using Fisher's Exact Test}$$

TABLE VI Relationships Among Punishment Frequency of Rape and Polygyny

Punishment	Polygyny present			Polygyny absent		
	Frequency of rape			Frequency of rape		
	Low	High	Total	Low	High	Total
Major	4	3	7	4	0	4
Minor	2	3	5	1	1	2
None	0	4	4	0	6	6
Total	6	10	16	5	7	12

$$\tau_c = -0.42 \text{ not significant}$$

$$\tau_c = -0.94 \text{ } P < 0.01 \text{ using Fisher's Exact Test}$$

50-50 chance) when they are absent major punishment and a high frequency of rape are not found to occur together. 3) Societies for which there is no punishment for rape have a high frequency of rape whether fraternal interest groups are present or absent (examine the lowest row of both sides of Tables V and VI).

These findings can be summarized in a paradigm which shows how the combinations of traits predict the frequency of rape found in a society.

major punishment + no fraternal interest groups → frequency of rape is low
 major punishment + fraternal interest groups → frequency of rape may be high or low

no punishment + no fraternal interest groups → frequency of rape is high
 no punishment + fraternal interest groups → frequency of rape is high

These findings indicate that while there is more support for deterrence theory than for fraternal interest group theory, neither theory alone gives as complete a picture as does a composite theory based upon the key independent variables in each of the separate theories.

CONCLUSION

The results of this cross-cultural study of rape have provided support for both fraternal interest group theory and deterrence theory, with stronger supporting evidence for the latter. Further analysis of the data, however, showed the usefulness — indeed I feel the necessity — of employing the key independent variables in a three variable analysis. Two conditions appear to be characteristic of societies in which there is no rape — major punishment and the absence of fraternal interest groups. Major punishment alone, however, does appear to be able to reduce the frequency of rape in a society. Moreover, it has been found that if there is no punishment the frequency of rape is high. Societies with fraternal interest groups have a high rape frequency if there is no punishment; however, if there is punishment, either major or minor, the frequency of rape may be either high or low. It appears, thus, that the presence of fraternal interest groups may override to some extent the influence of punishment in reducing the frequency of rape in a society. Nevertheless, the results suggest that strong sanctions decrease the frequency of rape, implying that penalties deter rape. It should also be pointed out that since the frequency of rape is high if punishment is absent and if fraternal interest groups are absent, the presence of fraternal interest groups alone does not predict rape.

Before the testing of the hypotheses, the author had predicted that fraternal interest group theory would receive support as it had in several other studies and that deterrence theory would not receive support for the same reason. The results thus came as a surprise.

From the analysis of the data a composite theory has emerged which combines the two theories which this study set out to test. The above paradigm summarizes the new theory. No encompassing social science expression such as deterrence or fraternal interest group theory is yet available to describe it. However, neither of the two theories initially tested has the explanatory power of the composite theory.

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social order the focus is often exclusively on the use of more and more sophisticated technology. At first this seems to be even handed liberal editorializing but on second reading it turns out to be either meaningless or an evasive defence of the status quo by the use of sermonial platitudes.

The remaining chapters are manuals for policy makers and police chiefs and they may be useful to both. One bit of advice (coming originally from L. C. Green who is not one of the authors but seems to be the source of many of their ideas) deserves to be quoted. Any attempt to cope with terrorism must be directed to the act rather than the actor so that sympathy for those who commit the alleged terrorist act must not be allowed to invalidate condemnation of the act. This certainly makes sense and it is a part of a general model of prevention suggested by the authors. A more serious scholarly discussion of the issue would have led them to ask when and where is that model followed and how. Most often as we well know attempts to divert attention from the actor to the act have failed. Only the completely ahistorical approach of the authors allows them to entertain seriously such suggestions. The recommendation has been given to many governments on unnumbered occasions of insurrection and restlessness. What government in recent memory has not condemned the criminal acts of a small band of terrorists? The people who have issued such statements have no PhDs in criminology sociology or psychology but they accept the great principle of separating the act from its context.

Chapter 5 is devoted to Problems of Institutionalizing Political Terrorism (as opposed to nonpolitical ones?) and is a brief manual for prison wardens on how to keep political prisoners under control in the most elegant way phrased in social science jargon. It reminded this reviewer of the memoirs of Russian revolutionaries imprisoned in the Peter and Paul fortress in St Petersburg in Czarist days. Those prisoners were well aware of the ideas contained in this chapter as were their wardens.

The chapters devoted to different countries contain some interesting information which may be of use as raw material but offers little in the way of critical analysis. The writers often sound like official representatives of their governments and for one (Erich Corves) that impression is confirmed by a government statement. One tends to suspect that scholars critical of their governments were not invited to the conference. Of special interest are Chapter 12 (Political Prisoners and Terrorists in American Correctional Institutions) and Chapter 14 (Political Facts on Internment in Northern Ireland). Chapter 12 has only five and a half pages on the stated ground of lack of matter. Chapter 14 is the longest and the most unusual in the book. It was not presented at the original conference but is reprinted from a Northern Ireland periodical. The reasons for its inclusion are obscure for its frame of reference is totally different from that of the other chapters.

Now I turn to what the authors have avoided namely looking at a social phenomenon in its social and historical context

Terrorism in the past 15 years has outstepped its recognized borders to bring the horrors of insecurity and violence deep inside the First World. Stemming either from struggles between the First World (Western democracies) and the Third World or from internal upheavals and instability within those Western democracies every act of terrorism was a reminder of the gap between technological control which has been achieved and social domination which is still incomplete. The reaction of governments as the authors of this book point out was mostly technological. The authors have sought to prove that social control can be advanced as technological control. The book and the conference behind it then become a case study in the philosophy and practice of modern social science. When a problem is identified as social rather than moral or political there the social scientist is found seeking research grants and offering solutions. In this case when terrorism and skyjacking were seen as a problem for Western democracies somebody said Let's have a scholarly conference. The authors who are all scholars in the social science known as criminology secured financial support from the US and Canadian governments for a conference which brought together government officials legal scholars and criminologists. The legal scholars and the government officials as would be expected represented official viewpoints. From social science scholars we expect illumination and insight related to social phenomena. Instead we get a model of how not to do scholarly analysis. The guiding rule seems to be ignore the context of what you are looking at. No interest is shown in the background of terrorist acts since the goal is prevention and control not understanding. The goal is a better technology – a social technology presented by the social sciences to match that of the natural sciences.

W H Auden is reported to have said Thou shalt not commit social science. After reading this volume it is easy to see why.

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A History of Aggression in Freud by Paul Stepansky New York International Universities Press 1977 pp x + 201

This book traces the development of Freud's ideas about aggression and the part it plays in human behavior. It is a dense book full of psychoanalytic terminology of no use to the reader casually interested in psychoanalysis but directed to psychoanalysts or historians of psychoanalysis.

In 1908 Alfred Adler first wrote about what he called the *aggressive instinct* (German: *Trieb*). Not until eleven years later, in the year after the ending of the First World War, did Freud himself, in *Beyond the Pleasure Principle*, begin to write in terms of the aggressive instinct. According to the dust-cover, the aim of Stepansky's book is to dispel the mistaken belief that it was only the impetus of World War I that forcibly turned his attention to the importance of aggression. It is worth mentioning that at the beginning of 1920 Freud's daughter Sophie and Anton von Freund, Freud's friend and benefactor, died within a few days of each other, leaving Freud with what he described as a bitter, irreparable narcissistic hurt and morbid fears about his own ultimate death.

Stepansky convincingly shows that Freud rated highly the importance of aggression in personality development long before these events. Certainly, by the time he was beginning to write about the Oedipus complex in the *Interpretation of Dreams* in 1900, the role of aggression became central to Freud's thinking. Stepansky makes the important point that the Oedipus myth was invoked originally to explain not infantile sexuality but fantasied aggression such as the death wish occurring in dream life.

The First World War, far from focussing Freud's attention on aggression, so appalled and frightened him that he was driven to rationalise in terms of biology the need for this explosion of irrational and destructive behavior. In an open letter to Einstein, Freud wrote: 'War is in the crassest opposition to the psychological conditions imposed on us by the presence of civilisation and for that reason we are bound to rebel against it — we simply cannot any longer put up with it.'

At first, Stepansky suggests, Freud tried to deal with the terrible feelings that the First World War produced in him by talking about a healthy, hating ego. The ability of the ego to hate was seen as necessary to help it in its struggle to preserve and maintain itself (*Instincts and Their Vicissitudes*, 1915).

The First World War could then be seen as a perverted but biologically understandable struggle for survival. By the time of publishing *Beyond the Pleasure Principle* in 1920, Freud had gone even further in taking the sting out of his aggressiveness by suggesting that it was an aspect of his newly discovered death instinct. Freud here began to talk in what Stepansky describes as obscure terms. By now, life had become merely a circuitous path returning to the existence called by Freud the *Nirvana Principle* (adopting a term coined by

a Low) He no longer thought of war as tapping an immanent aggressiveness but as anticipating an inevitable entropy. Thus war became the result of the external influences acting through biological drives outside Man's control. In the middle of the book Stepansky begins to discuss Freud's views with Adler. This makes interesting reading but would have made more sense in a separate essay (Stepansky is writing a book about Adler). Stepansky says that Freud over reacted to Adler and indeed misinterpreted him. In a note to Adler's work in the Little Hans history Freud wrote "I cannot help myself to assume the existence of a special aggressive instinct alongside of similar instincts of self preservation and sex and on an equal footing with them". In fact Adler was not particularly interested in the Freudian concept of aggression or otherwise. Adler's was an ego psychology: children suffer from a sense of inferiority because they *are* inferior to adults (in strength and knowledge) and their personality is moulded by masculine protest against their state of inferiority. Stepansky raises the question: why did Freud over react to Adler's ideas? The answer he gives is that for Freud Adler was a revenant of his younger brother Julius who lived only a few months. This death left Freud with feelings of great power but with terrifying feelings about the possible effects of his own aggressiveness. When Freud began to see that Adler's ideas were diverging from his own he rationalized his resulting fury by dismissing Adler's ideas on the theoretical grounds that Adler's work over-emphasized the importance of aggression at the expense of sexuality. Hence even the founder of psychoanalysis was not immune to the human tendency to project unwanted thoughts and feelings on the others. This is a general criticism of psychoanalysis that its methods of investigation are inevitably influenced by the psychodynamics of its practitioners. Stepansky also raises a question not answered by him at all: can psychoanalysis be said to be a scientific discipline? This is a scholarly and very thoroughly researched book to be of considerable value to students of psychoanalysis but the account it gives of the development of Freud's ideas would I fear confirm all the fears of those who are already sceptical about psychoanalytical concepts and technique.

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England

A Guide to the Literature on Aggressive Behavior

Articles relating to the general problem area of aggression are scattered throughout the whole range of specialized journals in fields from A for Anatomy to Z for Zoology. It is virtually impossible for a single individual to find all the articles which may bear on his particular interest. Information overload is of course a problem. However, an even greater problem is matching the interesting article with the interested reader. *Aggressive Behavior* will attempt to alleviate this problem by publishing a list of references in each issue. The reference list will be compiled from several sources. Each article indexed in *Psychological Abstracts* and indexed under the following terms will be included:

- 1 Aggressive Behavior
- 2 Anger
- 3 Animal Aggressive Behavior
- 4 Attack Behavior
- 5 Hostility
- 6 Threat Postures
- 7 Violence
- 8 Frustration
- 9 Conflict

Each reference will be coded according to the index terms listed above and will be listed in alphabetical order by senior author. There are a large number of journals that publish articles related to aggression that are not covered by *Psychological Abstracts*. In order to find such references, the cooperation of all readers of this journal is needed. If each of the several hundred investigators concerned with the problem of aggression makes a habit of contributing to the literature search section of *Aggressive Behavior*, the search task of each of us will be made easier. If in your coverage of the literature you find an article not indexed in a journal that is not regularly abstracted by *Psychological Abstracts*, please send the full reference on a 3 X 5 card and send it to the editor for inclusion in the literature search section.

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